

An annotated catalogue of type specimens of the land snail genus *Cyclophorus* Monfort, 1810 (Caenogastropoda, Cyclophoridae) in the Natural History Museum, London

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Abstract

The collection of land caenogastropod snails in the genus *Cyclophorus* Monfort, 1810 housed in the Natural History Museum, London (NHM), includes 52 type lots. Lectotypes have been designated for 43 available species-level names to stabilize existing nomenclature, two previously designated lectotype, two holotypes, one paratype, one syntype, one possible syntype and two paralectotypes are also listed. A complete catalogue of the *Cyclophorus* types in NHM, London is provided for the first time.

Keywords

Gastropoda, type specimens, biohistory, NHM, taxonomy, land snails, Cyclophoridae, *Cyclophorus*

Introduction

The Cyclophoridae Gray, 1847 are a family of caenogastropod land snails with a fossil history dating back to the Early Tertiary (Gordon and Olson 1995). Extant cyclophorids are distributed in Africa, Asia, Australia, Southern Europe and various Pacific islands (Ko-

belt 1902, 1907–1908, Solem 1959, Stanisic 1998). Kobelt (1902, 1907–1908) carried out detailed reviews of the extensive nineteenth century literature on the Cyclophoroidea (= Cyclophoridae sensu Kobelt 1902); his work remains the standard reference for the group based on shell morphology. Subsequent work combined shell morphology with soft body anatomy, but intra- and interspecific variation in shell morphology within the Cyclophoridae, combined with a highly conserved soft body anatomy, resulted in little progress (Tielecke 1940, Andrews and Little 1972, Stanisic 1998, Barker 2001). Recent classifications of the Cyclophoridae have recognised three subfamilies: Cyclophorinae, Alycaeinae, and Spirostomatinae (Bouchet and Rocroi 2005). Thirty five genera containing approximately 810 species have been recognized in the Cyclophoridae (Kobelt 1902, 1907–1908, Wenz 1938, Vaught 1989, Bouchet and Rocroi 2005, Lee et al. 2008).

With about 22% of the species, *Cyclophorus* Monfort, 1810 is the most species rich genus in the Cyclophoridae amounting to about 180 nominal species (Kobelt 1902, 1908). *Cyclophorus* is distributed through the humid or seasonally humid tropical and warm temperate habitats of South Asia and SE Asia, including the southern areas of China, Korea and Japan (Kobelt 1902, 1907–1908, Gude 1921, Pilsbry 1926, Bentham Jutting 1948, 1949, Solem 1959, Minato and Habe 1982). Kobelt (1902) divided *Cyclophorus* into eight subgenera using shell size, shell shape, features of the peristome, umbilicus, and their geographical distribution. Subsequently Wenz (1938) recognized seven subgenera and then Vaught (1989) recognized only six subgenera. *Cyclophorus* species limits are generally poorly established. Some attempts have been made to provide a more secure basis for recognizing species limits using soft body anatomy and cytogenetic analysis (Welber 1925, Tielecke 1940, Andrews and Little 1972, Kasinathan 1975, Kongim et al. 2006). Most recently, Nantararat et al. (2014) clarified some relationships and species limits within *Cyclophorus* by using DNA sequences and constructing molecular trees.

Cyclophorus species level taxa were described solely on the basis of shell morphology and most of them were described without illustrations or designation of holotypes. The most prolific author of *Cyclophorus* species was O.F. Möllendorff, who described about 14% (26 taxa) of all *Cyclophorus* taxa. His type specimens housed in the Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt were catalogued and illustrated by Zilch (1956). The other major contributors to descriptions of *Cyclophorus* species were L. Pfeiffer, H.H. Godwin-Austen, G.B. Sowerby I. and E.A. Smith. Most of the *Cyclophorus* species that they described are housed in the Natural History Museum, London (hereafter the Museum or NHM) and account for about 30% (58 taxa) of the *Cyclophorus* taxa (Kobelt 1902, 1907–1908, Gude 1921, Pilsbry 1926, Bentham Jutting 1948, 1949, Solem 1959, 1966, Minato and Habe 1982).

The Museum holds one of the largest collections of Mollusca in the world, rich in type specimens it is also one of the most important natural history collection. Dating back to 1753 the collections abound with historical material (MacLellan and Way 2012). As with any museum collection with a long history, the documentation of specimens is sometimes in a poor state and records may contain conflicting information such that the recognition of some type material is problematic. We have critically evaluated the type status of material by comparing specimens, labels with the speci-

mens, information in the registers, and information provided in the original descriptions. Of notable value are the distinctive handwritten labels of Pfeiffer and 'MC', indicating that the lot was part of the Hugh Cuming collection (Breure and Ablett 2011). Syntype status can be established with different degrees of confidence, largely depending on the quality of information on specimen labels and information provided in the registers. Labels handwritten by the original author verifying type status appear to provide unequivocal evidence but there remained a possibility that specimens could have been mixed up and placed with the wrong labels and all specimens selected as lectotypes were carefully compared with the original description, original figures when available, and with any measurements provided in the original description. Type localities are cited as in original descriptions. Additional information from labels, current political boundaries or subsequently published localities is given in square brackets.

Method

Specimens were photographed showing apertural, apical and umbilical views. Shell measurements were made for the adult specimen using digital calipers. The adult shell specimens are easy to be distinguished from juveniles by performing expanded and reflexed apertural lips. The specimen was measured accurately to 0.1 mm, and the expanded lip of aperture was included. Shell height (H) was measured along the columellar axis passing through apex to apertural base. Shell width (W) is the maximum width perpendicular to columella axis (Cox 1960: fig. 80). Numbers of whorl were counted, from the shell apex where incidence of the spiral sculpture approaches 90° as follow Burch and Pearce (1990: fig. 6).

Abbreviations: Material was examined from the following institutions: NHM, The Natural History Museum, London (NHM registered specimens are cited as NHMUK); MCZ, Museum of Comparative Zoology, Harvard University, Cambridge. Others abbreviations used are: D, shell diameter; H, shell height; W, number of whorls.

Catalogue of the type specimens of *Cyclophorus* Montfort, 1810

Cyclophorus aborensis Godwin-Austen, 1915

http://species-id.net/wiki/Cyclophorus_aborensis

Cyclophorus aborensis Godwin-Austen, 1915: 494, pl. 38, fig. 1. Gude 1921: 69

Type locality. Rotung, 2000 ft., near Egar stream; Kalek and Renging, 2000 ft.

Type material. Lectotype (design. n.), NHMUK 1903.7.1.3051 from Renging (Fig. 2A; D=52.5 mm, H=40.2 mm, W=5), paralectotypes NHMUK 1903.7.1.3048 from Kalek (2 shells; Fig. 2B; D=49.1 mm, H=34.0 mm, W=5; D=48.6 mm, H=36.0 mm, W=5). NHMUK 1903.7.1.3049 from Rami Dambang, Abor (2 shells; D=33.0 mm, H=24.4 mm, W=5; D=29.6 mm, H=21.8 mm, W=5).

Remarks. Godwin-Austen clearly states that this taxon was based on five lots of specimens from various localities. The original description included illustrations of two specimens from different localities, but only one set of measurement was given. In addition, the author clearly stated that two lots of the type series were kept in the Indian Museum, and the remaining three type lots were housed in the NHM. The specimen NHMUK 1903.7.1.3051 with Godwin-Austen handwriting label stating “Co-type” and figured in the original description (Godwin-Austen 1915: figs 1, 1a) is here designated as the lectotype. The other 2 specimen lots housed in the NHM (nos. 3048 and 3049), and the two lots previously housed in the Indian Museum, that were transferred to the Zoological Survey of India (nos. 6009 and 6010), are therefore paralectotypes. Following our lectotype designation, the type locality of this species is fixed as Renging, Abor Hills (altitude 2000 ft.) (ICZN 1999: Art. 76.2).

***Cyclophorus affinis* Theobald, 1858**

http://species-id.net/wiki/Cyclophorus_affinis

Cyclophorus affinis Theobald, 1858: 246. Hanley and Theobald 1870: 1, 28, pl. 2, fig. 7 and pl. 48, fig. 2. Kobelt 1902: 135. Kobelt 1908: 654.

Type locality. Maulmein [Mawlamyine, Myanmar].

Type material. Lectotype (design. n.), NHMUK 1903.7.1.1454 (Fig. 2C; D=34.9 mm, H=28.7 mm, W=5).

Remarks. The original description stated this taxon was based on two individuals, and gave the dimensions of both specimens. The single specimen from the Godwin-Austen collection, purchased from Theobald, closely matches the larger of the two measurements given in the original description and figured in Hanley and Theobald (1870: pl. 2, fig. 7). This specimen is designated as the lectotype. The type specimen relating to the smaller of the two measurements could not be located in the NHM collections.

***Cyclophorus amoenus* (Pfeiffer, 1854)**

http://species-id.net/wiki/Cyclophorus_amoenus

Cyclostoma (Cyclophorus) amoenum Pfeiffer, 1854b [1852]: 62. Pfeiffer 1854a: 346, pl. 45, figs 11, 12.

Cyclophorus amoenus – Reeve 1861: sp. 40. Kobelt 1902: 97.

Type locality. unknown.

Type material. Lectotype (design. n.), NHMUK 20130113/1 (Fig. 3A; D=30.0 mm, H=23.5 mm, W=4½), paralectotype NHMUK 20130113/2 (1 shell; Fig. 3B; D=26.0 mm, H=22.5 mm, W=4½).

Remarks. This species was described based on specimens from the Cuming collection. In the original description only one set of specimen measurements was given. In 1854, Pfeiffer (1854a: 346, pl. 45, figs 11, 12) re-published the description and illustrated a single specimen from the Cuming collection. There are two specimens from the Cuming collection with an original label in Pfeiffer's handwriting stating the species name, and a subsequent label stating "Type". The figured specimen in Pfeiffer (1854a) can be recognized by the varix on the last whorl, and is designated here as the lectotype.

***Cyclophorus appendiculatus* (Pfeiffer, 1854)**

http://species-id.net/wiki/Cyclophorus_appendiculatus

Cyclostoma (*Cyclophorus*) *appendiculatum* Pfeiffer, 1854b [1852]: 61. Pfeiffer 1854a: 345, pl. 45, figs 7, 8.

Cyclophorus appendiculatus – Kobelt, 1902: 106. Kobelt 1907: 584.

Type locality. Insulis Philippinis [Philippines].

Type material. Lectotype (design. n.), NHMUK 20130079/1 (Fig. 3C; D=34.3 mm, H=20.1 mm, W=4½), paralectotypes NHMUK 20130079/2-3 (2 shells, Fig. 3D; D=32.1 mm, H=19.8 mm, W=4½ and D=34.4 mm, H=21.8 mm, W=4½).

Remarks. This species was described based on specimens from the Cuming collection. In the original description only one set of specimen measurements was given. In 1854, Pfeiffer (1854a: 345, pl. 45, figs 7, 8) re-described and illustrated a single specimen from the Cuming collection. There are three specimens from the Cuming collection with an original label in Pfeiffer's handwriting stating the species name. The figured specimen in Pfeiffer (1854a) closely matches the measurements given in the original description and is here designated as the lectotype.

***Cyclophorus aquilus* (Sowerby I, 1843)**

http://species-id.net/wiki/Cyclophorus_aquilus

Cyclostoma aquilum Sowerby I, 1843b: 61 [March]. Sowerby I 1843c: 123, pl. 27, fig. 131 [June]. Pfeiffer 1846: 14, pl. 8, figs 1, 2.

Cyclophorus aquilus – Reeve 1861: sp. 45. Kobelt 1902: 124. Kobelt 1907: 578.

Type locality. Singapore.

Type material. Lectotype (design. n.), NHMUK 20110225/1 (Fig. 3E; D=39.9 mm, H=31.7 mm, W=5), paralectotypes NHMUK 20110225/2-3 (2 shells; Fig. 3F; D=38.7 mm, H=29.5 mm, W=5, and D=39.9 mm, H=31.2 mm, W=5).

Remarks. A figure was not provided in the original description but a figure in "Thes. Conch. part 3, pl. 27, fig. 131" was cited. The original description states 'Found in the Woods at Singapore under decayed leaves by H. Cuming'. There are three specimens from the Cuming collection with an original label, possibly in Sowerby's

handwriting that states ‘Singapore in the wood under decayed leaves’. We therefore recognize these specimens as syntypes and the figured specimen (Sowerby I 1843c: pl. 27, fig. 131) is here designated as the lectotype.

***Cyclophorus bapuensis* Godwin-Austen, 1915**

http://species-id.net/wiki/Cyclophorus_bapuensis

Cyclophorus (Glossostylus) bapuensis Godwin-Austen, 1915: 494, 495, pl. 38, fig. 2.
Gude 1921: 57.

Type locality. Abor Hills, vicinity of Bapu. [Arunachal Pradesh, India].

Type material. Lectotype (design. n.), NHMUK 1903.7.1.3108/1 (Fig. 4A; D=32.3 mm, H=23.7 mm, W=5), paralectotypes NHMUK 1903.7.1.3108/2-3 (2 shells; Fig. 4B; D=30.3 mm, H=22.3 mm, W=5, and D=30.0 mm, H=22.4 mm, W=5).

Remarks. The original description stated “Type no. 3108 Brit. Mus.” There are three specimens in the type lot number 3018 from the Godwin-Austen collection. The specimen figured in the original description corresponds to the measurements given in the original description and is here designated as the lectotype.

***Cyclophorus beddomeanus* Preston, 1914**

http://species-id.net/wiki/Cyclophorus_beddomeanus

Cyclophorus beddomeanus Preston, 1914: 21, text-fig. Gude 1921: 74, 75.

Type locality. Naga Hills [Assam, Arunachal Pradesh and Nagaland, India].

Type material. Lectotype (design. n.), NHMUK 1936.4.15.22 (Fig. 4C; D=53.8 mm, H=44.0 mm, W=5).

Remarks. The original description gives a range of shell dimensions so this species is clearly based on more than one specimen. Preston mentions a “white-lipped variety” that was included in the type series but which could not be located in the NHM collections. The specimen 1936.4.15.22 is the one figured in the original description and is designated as the lectotype.

***Cyclophorus bensoni* (Pfeiffer, 1854)**

http://species-id.net/wiki/Cyclophorus_bensoni

Cyclostoma bensoni Pfeiffer, 1854c [1852]: 158. Pfeiffer 1853a: 244, pl. 32, figs 11–13.
Cyclophorus bensoni – Hanley and Theobald 1870: 16, pl. 34, fig. 5. Kobelt 1902: 108.

Type locality. unknown.

Type material. Lectotype (design. n.), NHMUK 20130115 (Fig. 4D; D=42.8 mm, H=35.5 mm, W=5).

Remarks. This species was described based on specimens from the Cuming collection. In the original description only one set of specimen measurements was given. In 1853, Pfeiffer (1853a: 244, pl. 32, figs 11–13) re-described and illustrated a single specimen from the Cuming collection. There is a single specimen from the Cuming collection with an original label in Pfeiffer's handwriting stating the species name. The figured specimen in Pfeiffer (1853a) closely matches the measurements given in the original description and is here designated as the lectotype.

***Cyclophorus cochranei* Godwin-Austen, 1889**

http://species-id.net/wiki/Cyclophorus_cochranei

Cyclophorus cochranei Godwin-Austen, 1889: 334, 335. Smith 1895: 119, pl. 4, fig. 2. Kobelt 1902: 127.

Type locality. Niah Hills [Sarawak, Malaysia].

Type material. Lectotype (design. n.), NHMUK 1889.12.7.5 (Fig. 5A; D=40.8 mm, H=29.9 mm, W=5).

Remarks. In the original description, Godwin-Austen states there were three specimens, one from Niah Hills and two from Busan Hills. The NHM collections contain a single specimen from Busan Hills with a "T." written on the shell. It matches the measurements given in the original description and is designated as the lectotype. The two other specimens (one from Busan, one from Niah Hills) could not be located in the NHM collections.

***Cyclophorus consociatus* Smith, 1893**

http://species-id.net/wiki/Cyclophorus_consociatus

Cyclophorus consociatus Smith, 1893: 13. Kobelt 1902: 109.

Type locality. Annam [Central Vietnam].

Type material. Lectotype (design. n.), NHMUK 1893.2.26.8 (Fig. 5B; D=39.0 mm, H=34.0 mm, W=5), paralectotypes NHMUK 1893.2.26.9-10 (2 shells; Fig. 5C; D=36.9 mm, H=31.0 mm, W=5, and D=26.1 mm, H=21.8 mm, W=5).

Remarks. There are three specimens in the type lot with original labels in Smith's handwriting including a label stating "type", and subsequently changed to read "holotype red spot". The original description gives the measurements of only one shell which matches those of the NHM specimen with the red spot. This specimen is designated as the lectotype.

***Cyclophorus crassalabella* Godwin-Austen, 1888**

http://species-id.net/wiki/Cyclophorus_crassalabella

Cyclophorus crassalabella Godwin-Austen, 1888: 244. Kobelt 1902: 110.

Type locality. Shan Hills [Shan State, Myanmar].

Type material. Lectotype (design. n.), NHMUK 1911.6.10.8 (Fig. 5D; D=41.5 mm, H=30.7 mm, W=5).

Remarks. The original description gives the measurements of only one shell which matches those of the NHM specimen. The original label also states “P.Z.S. 1888 TYPE” in Godwin-Austen’s hand writing. This specimen is designated as the lectotype.

***Cyclophorus cucullata* (Gould, 1856)**

http://species-id.net/wiki/Cyclophorus_cucullata

Cyclostoma cucullata Gould, 1856: 14.

Cyclophorus cucullatus – Reeve 1861: sp.44. Kobelt 1902: 127. Johnson 1969: 63.

Type locality. Mergui Archipelago [Myanmar].

Type material. Lectotype MCZ 169108, paralectotypes MCZ 169109 (1 shell) and NHMUK 20130116 (2 shells; Fig. 6A, B; D=27.2 mm, H=20.1 mm, W=5; D=26.5 mm, H=21.8 mm, W=5).

Remarks. Johnson (1964: 63) stated “holotype, MCZ 169108”, which we consider to be a valid inadvertent lectotype designation (ICZN 1999: Art. 74.5). Pfeiffer (1858: 44) provided the description of this species based on Cuming collection material which he listed as “*Cyclostoma cucullata* Gould, MS” indicating that specimens under the manuscript name were presented to Cuming by Gould. In addition, Johnson (1964) confirms Gould met Cuming around 1857 leaving some specimens of his new species with Cuming. Later, Reeve (1861: sp. 44) re-published Pfeiffer’s description, and included illustrations of a specimen from the Cuming collection. There are two specimens in the NHM, one is the shell figured in Reeve (1861: sp. 44), with an original label stating “type”, and the locality is given as “Mergui Archipelago” Therefore, the NHM specimens received from Gould forms part of the type series and are paralectotypes.

***Cyclophorus eudeli* Smith, 1893**

http://species-id.net/wiki/Cyclophorus_eudeli

Cyclophorus eudeli Smith, 1893: 13. Kobelt 1902: 137.

Type locality. Annam [Central Vietnam].

Type material. Lectotype (design. n.), NHMUK 1893.2.26.5 (Fig. 6B; D=40.0 mm, H=33.0 mm, W=5½), paralectotypes NHMUK 1893.2.26.6-7 (2 shells: 1 adult and 1 juvenile; Fig. 6C; D=40.1 mm, H=32.1 mm, W=5½).

Remarks. The original description was clearly based on more than one specimen since it states “in examplis” (“in examples”) although only one set of shell measurements was given. There are three specimens in the NHM lot with an original label in Smith’s handwriting. The specimen that most closely matches measurements given in the description is designated as the lectotype.

Cyclophorus everetti Smith, 1892

http://species-id.net/wiki/Cyclophorus_everetti

Cyclophorus everetti Smith, 1892: 343, pl. 25, fig. 5. Kobelt 1902: 128. Kobelt 1908: 688.

Type locality. Barit Mountain [north of Borneo, Malaysia].

Type material. Lectotype (design. n.), NHMUK 1892.7.20.103 (Fig. 6D; D=36.7 mm, H=20.1 mm, W=4½), paralectotypes NHMUK 1892.7.23.1-2 (2 shells: 1 adult and 1 juvenile; Fig. 6E; D=33.6 mm, H=20.2 mm, W=4½).

Remarks. Vermeulen (1999: 141) noted that the type specimens would be housed in the NHM, London but that he had not seen the specimens. We found four specimens of this species from Everett’s collection with original labels in Smith’s handwriting. This lot contained a juvenile specimen as was indicated in the original description. The figured specimen matches with the single set of shell measurements given in the original description and is designated as the lectotype.

Cyclophorus exaltatus (Pfeiffer, 1855)

http://species-id.net/wiki/Cyclophorus_exaltatus

Cyclostoma (*Cyclophorus*) *exaltatum* Pfeiffer, 1855b [1854]: 300.

Cyclophorus exaltatus – Kobelt 1902: 138. Kobelt 1908: 625.

Type locality. Hong Kong, China.

Type material. Lectotype (design. n.), NHMUK 1980041/1 (Fig. 7A; D=25.1 mm, H=25.3 mm, W=5), paralectotypes NHMUK 1980041/2-3 (2 shells; Fig. 7B; D=24.6 mm, H=24.4 mm, W=5 and D=23.3 mm, H=23.4 mm, W=5).

Remarks. The NHM type lot was collected by Mr. Fortune and is from Cum-
ing’s collection as stated in the original description. It has an original label in Pfeiffer’s handwriting giving the species name and collection locality. The specimen that most closely matches measurements given in the original description is here designated as the lectotype.

***Cyclophorus excellens* (Pfeiffer, 1855)**

http://species-id.net/wiki/Cyclophorus_excellens

Cyclostoma (*Cyclophorus*) *excellens* Pfeiffer, 1855a [1854]: 126, 127.

Cyclophorus excellens – Pfeiffer 1854e: 11, pl. 4, figs 1, 2. Kobelt 1902: 128. Kobelt 1908: 670.

Type locality. Unknown.

Type material. Lectotype (design. n.), NHMUK 20130084/1 (Fig. 7C; D=52.5 mm, H=35.9 mm, W=5), paralectotype NHMUK 20130084/2 (1 shell; Fig. 7D; D=44.0 mm, H=31.3 mm, W=5).

Remarks. This species was described based on material from the Cuming collection, and only one set of shell measurement was given. Later, Pfeiffer (1854e: pl. 4, figs 1, 2) re-published the description and figured a shell from the Cuming collection. Two shells from Cuming's collection with an original label in Pfeiffer's handwriting giving the species name are in the NHM collections. The specimen which most closely matches the measurements given in the original description and the illustration in Pfeiffer (1854e) is here designated as the lectotype.

***Cyclophorus expansus* (Pfeiffer, 1853)**

http://species-id.net/wiki/Cyclophorus_expansus

Cyclostoma expansum Pfeiffer, 1853b [1851]: 242. Pfeiffer 1854a: 293, pl. 39, figs 20, 21.

Cyclophorus expansus – Reeve 1861: sp. 18. Hanley and Theobald 1870: 1, pl. 2, figs 3, 4. Kobelt 1902: 129. Kobelt 1908: 656.

Type locality. unknown.

Type material. Lectotype (design. n.), NHMUK 20130086/1 (Fig. 7E; D=30.1 mm, H=25.5 mm, W=5), paralectotypes NHMUK 20130086/2-3 (2 shells; Fig. 7F; D=29.9 mm, H=25.8 mm, W=5; D=27.3 mm, H=23.7 mm, W=5).

Remarks. The original description did not include an illustration or collection locality. Pfeiffer subsequently (1854a: 293, pl. 39, figs 20, 21) re-published the description and figured the species. There are three shells from Cuming's collection with an original label in Pfeiffer's handwriting. The specimen which most closely matches with the measurements given in the original description and the illustration in Pfeiffer (1854a) is here designated as the lectotype.

***Cyclophorus fulguratus* (Pfeiffer, 1854)**

http://species-id.net/wiki/Cyclophorus_fulguratus

Cyclostoma (*Cyclophorus*) *fulguratum* Pfeiffer, 1854b [1852: 63]. Pfeiffer 1854a: 345, pl. 45, figs 9, 10.

Cyclophorus fulguratus – Reeve 1861: sp. 35. Kobelt 1902: 112.

Type locality. unknown

Type material. Lectotype (design. n.), NHMUK 20130117/1 (Fig. 8A; D=28.6 mm, H=25.4 mm, W=5), paralectotypes NHMUK 20130117/2-3 (2 shells; Fig. 8B; D=27.4 mm, H=25.1 mm, W=5; D=29.7 mm, H=25.7 mm, W=5).

Remarks. The original description by Pfeiffer did not give an illustration of the species or a collection locality. Pfeiffer (1854a: 354, pl. 45, figs 9, 10) re-published the description and figured the species. Three shells from Cuming's collection have an original Pfeiffer label giving the species name and a collection locality of "Arva", that could perhaps be in Pfeiffer's handwriting, although a later label states: "Arva" added to label not by Pfeiffer? In addition there is a separate label with the specimens, also possibly in Pfeiffer's handwriting, stating: 'Prame Pegu'. The figured shell from Pfeiffer (1854a: pl. 45, figs 9, 10) with an "x" written in the aperture is here designated as the lectotype but the type locality remains uncertain.

***Cyclophorus fultoni* Godwin-Austen & Beddome, 1894**

http://species-id.net/wiki/Cyclophorus_fultoni

Cyclophorus fultoni Godwin-Austen & Beddome, 1894: 508. Kobelt 1902: 129.

Type locality. Khasi Hills [Meghalaya, India].

Type material. Lectotype (design. n.), NHMUK 1894.6.20.1 (Fig. 8C; D=49.2 mm, H=32.8 mm, W=5).

Remarks. Godwin-Austen stated that he received three specimens from Mr. Fulton. Only one specimen from Hugh Fulton could be located in the NHM collections. The specimen has an original Godwin-Austen label stating "Type" and the shell closely matches with the measurements given in the original description. It is here designated as the lectotype.

***Cyclophorus fuscicolor* Godwin-Austen, 1876**

http://species-id.net/wiki/Cyclophorus_fuscicolor

Cyclophorus fuscicolor Godwin-Austen, 1876: 173, pl. 8A, fig. 1. Kobelt 1902: 112.

Type locality. Daffa Hills [Arunachal Pradesh and Assam, India].

Type material. lectotype (design. n.), NHMUK 1903.7.1.1452/1 (Fig. 9A; D=57.5 mm, H=44.8 mm, W=6), paralectotype NHMUK 1903.7.1.1452/2 (1 shell; Fig. 9B; D=50.1 mm, H=40.5 mm, W=6).

Remarks. The original description stated “in some specimens”, which implied that this taxon was based on more than one specimen. There are two specimens from the Godwin-Austen collection with “Type” written on the original label. The specimen figured in the original description is here designated as the lectotype.

***Cyclophorus haughtoni* Theobald, 1858**

http://species-id.net/wiki/Cyclophorus_haughtoni

Cyclophorus haughtoni Theobald, 1858: 246. Hanley and Theobald 1870: 1, pl. 1, fig. 3, pl. 3 fig. 6 and pl. 48, fig. 6. Kobelt 1902: 129. Kobelt 1908: 661.

Type locality. Maulmein [Mawlamyine, Myanmar].

Type material. Lectotype (design. n.), NHMUK 1888.12.4.1953 (Fig. 10A; D=42.0 mm, H=36.9 mm, W=5), paralectotype NHMUK 1888.12.4.1954 (1 shell; Fig. 10B; D=41.8 mm, H=32.4 mm, W=5).

Remarks. This species was based on more than one specimen, from Theobald’s collection but only one set of measurement was given. The original description did not include an illustration but subsequently, Hanley and Theobald (1870) figured three illustrations of this species. There are two shells in the NHM collections purchased from W. Theobald, with an original label stating “typical”, and with the collection locality “Moulmein”. The specimen that most closely matches the measurements given in the original description, and the illustration in Theobald (1870: pl. 1, fig. 3 and pl. 48, fig. 6) is designated as the lectotype.

***Cyclophorus himalayanus* (Pfeiffer, 1853)**

http://species-id.net/wiki/Cyclophorus_himalayanus

Cyclostoma himalayanum Pfeiffer, 1853b [1851]: 242. Pfeiffer 1853a: 247, pl. 33, figs 10, 11. *Cyclophorus himalayanus* – Kobelt 1902: 112. Kobelt 1908: 674.

Type locality. Himalayâ [Himalaya, India].

Type material. Lectotype (design. n.), NHMUK 20130118 (Fig. 10C; D=48.0 mm, H=41.1 mm, W=5).

Remarks. This species was described from specimens in the Cuming collection and only one set of shell measurements was given in the original description. Pfeiffer (1853a: 247, pl. 33, figs 10, 11) republished the description and figured a shell from Cuming’s collection. There is a single shell in the NHM collections from the Cuming collection with an original label stating “the type” which exactly matches Pfeiffer illustration (1853a) and is here designated as the lectotype.

***Cyclophorus ibyatensis* (Pfeiffer, 1854)**

http://species-id.net/wiki/Cyclophorus_ibyatensis

Cyclostoma (*Cyclophorus*) *ibyatense* Pfeiffer, 1854b [1852]: 62. Pfeiffer 1854a: 349, pl. 45, figs 19, 20.

Cyclophorus ibyatensis – Reeve, 1861: sp. 48. Kobelt 1902: 139.

Type locality. Insula Ibyat “Bashee group” [Itbayat Island, Batanes Islands, Philippines].

Type material. Lectotype (design. n.), NHMUK 20130081/1 (Fig. 11A; D=23.0 mm, H=17.7 mm, W=5), paralectotype NHMUK 20130081/2 (1 shell; Fig. 11B; D=22.0 mm, H=17.9 mm, W=5).

Remarks. This species was described from specimens in the Cuming collection and only one set of shell measurements was given in the original description. Pfeiffer (1854a: 349, pl. 45, figs 19, 20) republished the description and figured a shell from Cuming’s collection. There are two shells in the NHM collections with an original label in Pfeiffer’s handwriting giving the species name and original collection locality. The specimen which matches the illustration in Pfeiffer (1854a) and the dimensions given in the original description is here designated as the lectotype.

***Cyclophorus implicatus* Bavay & Dautzenberg, 1908**

http://species-id.net/wiki/Cyclophorus_implicatus

Cyclophorus implicatus Bavay & Dautzenberg, 1908: 249. Bavay and Dautzenberg 1909: 285, 286, pl. 9, figs 5–7.

Type locality. Muong Bo, Binh-Lu [Vietnam].

Type material. Paralectotype NHMUK 20130087 from Muong-Bo (Fig. 11C; D=36.5 mm, H=26.4 mm, W=5).

Remarks. The original description does not include an illustration but later, Bavay and Dautzenberg (1909: 285, 286, pl. 9, figs 5–7) republished the description and included illustrations of the species. Fischer-Piette (1950: 176) wrote the “holotype, 37 mm” which we consider to be an inadvertent lectotype designation (ICZN 1999: Art. 74.5). The lectotype is housed in the Muséum National d’Histoire Naturelle, Paris. The NHM specimen from the R.B. Lucas collection (purchased from Dautzenberg) has an original label stating “Type” and giving the collection locality “Muong-Bo” and is considered to be a paralectotype. Further paralectotypes are housed in the Royal Belgian Institute of Natural Sciences, Brussels.

***Cyclophorus kinabaluensis* Smith, 1895**

http://species-id.net/wiki/Cyclophorus_kinabaluensis

Cyclophorus kinabaluensis Smith, 1895: 495, pl. 38, fig. 4. Kobelt 1902: 130.

Type locality. Kina Balu, N. Borneo

Type material. Lectotype (design. n.), NHMUK 1894.7.20.38 (Fig. 11D; D=45.1 mm, H=31.1 mm, W=4½), paralectotype NHMUK 1893.6.8.31 (1 shell; Fig. 11E; D=43.7 mm, H=27.3 mm, W=4½).

Remarks. There are two shells in the NHM collections with Smith's handwriting on the original label. One specimen has a small label with "Type" written on it attached inside the aperture. This specimen corresponds to the figured specimen and the measurements given in the original description and is here designated as the lectotype.

***Cyclophorus koboensis* Godwin-Austen, 1915**

http://species-id.net/wiki/Cyclophorus_koboensis

Cyclophorus (Glossostylis) koboensis Godwin-Austen 1915: 495, pl. 38, fig. 4. Gude 1921: 64.

Type locality. Abor Hills, Kobo, on right bank of Tsanspu or Brahmaputra.

Type material. Lectotype (design. n.), NHMUK 1903.7.1.3579/1 from Kobo, R.B. Brahmaputra, Assam (Fig. 12A; D=30.3 mm, H=21.2 mm, W=5), paralectotypes NHMUK 1903.7.1.3579/2–4 from Kobo, R.B. Brahmaputra, Assam (3 shells; Fig. 12B; D=31.3 mm, H=22.2 mm, W=5; D=32.4 mm, H=22.1 mm, W=5; D=30.6 mm, H=20.7 mm, W=5), NHMUK 1903.7.1.3045 from Ponging, Abor Hills (3 shells; D=33.4 mm, H=21.6 mm, W=5; D=34.1 mm, H=23.5 mm, W=5; D=31.0 mm, H=20.6 mm, W=5), NHMUK 1903.7.1.3117 from Yamney Valley, Abor Hills (2 shells; D=29.5 mm, H=18.6 mm, W=5; D=30.3 mm, H=19.7 mm, W=5).

Remarks. Godwin-Austen's description was based on five specimen lots with figures of shells from different lots provided in the original description. Three lots were listed as being housed in the NHM, and two lots in the Indian Museum, Calcutta. Each of the three NHM has original labels in Godwin-Austen's handwriting stating species name, collection locality and catalogue numbers. The figured specimen from the lot 1903.7.1.3579 labelled "cotype" is here designated as the lectotype.

***Cyclophorus labiosus* (Pfeiffer, 1854)**

http://species-id.net/wiki/Cyclophorus_labiosus

Cyclostoma (Cyclophorus) labiosum Pfeiffer, 1854d [1853]: 51.
Cyclophorus labiosus – Reeve 1861: sp. 32. Kobelt 1902: 100.

Type locality. Unknown.

Type material. Lectotype (design. n.), NHMUK 20130080 (Fig. 12C, D=42.2 mm, H=30.4 mm, W=5).

Remarks. This species was described from material in the Cuming collection, and the original description does not include an illustration. Later, Reeve (1861: sp. 32) re-described the species and illustrated a shell from the Cuming collection. There is a single shell in the NHM collections from the Cuming collection with an original label in Pfeiffer's handwriting. This shell matches the measurements given in the original description and figured in Reeve and is here designated as the lectotype.

Cyclophorus linguiferus (Sowerby I, 1843)

http://species-id.net/wiki/Cyclophorus_linguiferus

Cyclostoma linguiferum Sowerby I, 1843a: 31. Sowerby I 1843c: 125, pl. 29, fig. 198.

Pfeiffer 1849: 168, pl. 23, figs 1–3.

Cyclophorus linguiferus – Reeve 1861: sp. 23a, b.

Cyclophorus validus var. *linguifera* – Kobelt 1902: 121.

Type locality. Lobock, insulae Bohol [Loboc, Bohol, Philippines].

Type material. Lectotype (design. n.), NHMUK 20110269/1 from Loboc, Bohol Island, Philippines, (Fig. 12D; D=35.4 mm, H=31.5 mm, W=5), paralectotypes NHMUK 20110269/2-3 (2 shells; Fig. 12E; D=33.1 mm, H=26.6 mm, W=5; D=31.1 mm, H=26.9 mm, W=5).

Remarks. The original description included three varieties indicated with “var. a”, “var. b” and “var. c”. Sowerby I subsequently published *Thesaurus Conchyliorum* (Sowerby I 1843c) with Latin and English descriptions and associated illustrations. Pfeiffer (1849: pl. 23, figs 1–3) and Reeve (1861: sp. 23a, b) published illustrations of the species, however, neither author recognized or used the three varietal forms. These subsequent illustrations are matched with the specimens in the Cuming collection labelled as “var. a”. Therefore we believe this implies that “var. a” is the type series of *Cyclostoma linguiferum* s.s. and the specimens labelled as “var. b” and “var. c” are distinct variants and are therefore excluded from the type series of this nominal species (ICZN 1999: Art. 72.4.1). The specimen of “var. a” illustrated in Sowerby I (1843c: pl. 29, fig. 198), and closest to the dimensions given in the original description is here designated as the lectotype.

Measurements of specimens in the lots previously recognized as “var. b” to “var. c” are given for future reference:

“var. b.” NHMUK 20110270 from Loboc, Bohol Island [Philippines] (3 shells; D=32.6 mm, H=29.3 mm, W=5; D=32.1 mm, H=28.0 mm, W=5; D=30.1 mm, H=25.4 mm, W=5).

“var. c” NHMUK 20110271 from Loboc, Bohol Island [Philippines] (1 shell; D=30.3 mm, H=27.3 mm, W=5).

***Cyclophorus lingulatus* (Sowerby I, 1843)**

http://species-id.net/wiki/Cyclophorus_lingulatus

Cyclostoma lingulatum Sowerby I, 1843b: 64. Sowerby I 1843c: 126, pl. 29, figs 208–210.
Pfeiffer 1849: 168, pl. 26, figs 6–10.

Cyclophorus lingulatus – Reeve 1861: sp. 49. Kobelt 1902: 114. Kobelt 1907: 573.

Type locality. Island of Siquijod [Siquijor, Philippines]; Deleguete, Zebu Island [Cebu Island, Philippines]; Sibonga, Zebu Island [Cebu Island, Philippines]; Loboc, Bohol Island [Loboc, Bohol, Philippines]; Argao, Zebu Island [Argao, Cebu Island, Philippines].

Type material. Lectotype (design. n.), NHMUK 20110272/1 from island of Siquijod (Fig. 12F; D=21.3 mm, H=16.9 mm, W=4½), paralectotypes NHMUK 20110272/2-3 (2 shells; Fig. 12G; D=20.9 mm, H=17.5 mm, W=4½; D=20.0 mm, H=17.2 mm, W=4½).

Remarks. The original description included eight varieties indicated as “var. a” to “var. h.”, based on samples from various localities sampled by H. Cuming and cites an illustration in “Thesaurus Conchyliorum part 3, pl. 30, fig. 208”. This illustration matches the specimens in Cuming collection labelled as “var. a”. Therefore we believe this implies that “var. a” is the type series of *Cyclostoma linguiferum* s.s. and the specimens labelled as “var. b” to “var. h” are distinct variants and are therefore excluded from the type series of this nominal species (ICZN 1999: Art. 72.4.1). The specimen of “var. a” illustrated by Sowerby I (1843c: pl. 29, fig. 208) is here designated as the lectotype.

Measurements of specimens in the lots previously recognized as “var. b” to “var. h” are given here for future reference:

“var. b.” NHMUK 20110273 from Siquijod Island [Philippines] (3 shells; D=19.9 mm, H=15.8 mm, W=4½; D=20.6 mm, H=16.5 mm, W=4½; D=20.4 mm, H=16.1 mm, W=4½).

“var. c” NHMUK 20110274 from Deleguete, Zebu Island [Philippines] (3 shells; D=26.0 mm, H=20.9 mm, W=4½; D=23.6 mm, H=18.4 mm, W=4½; D=23.5 mm, H=18.5 mm, W=4½).

“var. d” NHMUK 20110275 from Deleguete, Zebu Island [Philippines] (3 shells; D=24.1 mm, H=18.6 mm, W=4½; D=24.5 mm, H=19.9 mm, W=4½; D=24.5 mm, H=18.2 mm, W=4½).

“var. e” NHMUK 20110276 from Sibonga, Zebu Island [Philippines] (3 shells; D=24.4 mm, H=19.3 mm, W=4 ½; D=22.4 mm, H=19.8 mm, W=4 ½; D=24.4 mm, H=19.6 mm, W=4 ½).

“var. f” NHMUK 20110277 from Loboc, Bohol Island [Philippines] (3 shells; D=25.6 mm, H=20.1 mm, W=4½; D=25.4 mm, H=20.4 mm, W=4½; D=24.9 mm, H=19.3 mm, W=4½).

“var. g” NHMUK 20110278 from Argao, Zebu Island [Philippines] (3 shells; D=24.4 mm, H=18.6 mm, W=4½; D=23.6 mm, H=19.8 mm, W=4½; D=23.4 mm, H=19.4 mm, W=4½).

“var. h” NHMUK 20110279 from Loboc, Bohol Island [Philippines] (3 shells; D=25.1 mm, H=19.6 mm, W=4½; D=25.6 mm, H=20.6 mm, W=4½; D=26.4 mm, H=20.9 mm, W=4½).

***Cyclophorus malayanus* (Benson, 1852)**

http://species-id.net/wiki/Cyclophorus_malayanus

Cyclostoma malayanum Benson, 1852: 269.

Cyclophorus malayanus – Reeve 1861: sp. 2. Kobelt 1902: 130. Kobelt 1908: 658.

Type locality. In montibus vallibusque Insularum Penang et Lancavi, necnon in Peninsula Malayana [In the mountains, the valleys of the islands of Penang and Langkawi, as well as the Peninsula Malaysia]

Type material. Syntypes NHMUK 20130089 (2 shells; Fig. 13A; D=43.5 mm, H=32.1 mm, W=5; D=47.0 mm, H=37.3 mm, W=5)

Remarks. The original description did not include an illustration but Reeve (1861: sp. 2) subsequently re-published the description with illustrations of a specimen from the Cuming collection. The NHM collection contains a lot of three specimens' from the Cuming collection labelled “Malay Peninsula”. A label reads “Mr. Benson has also sent me his *Malayanum* and the true *volvulus* for comparison...”. Two of the three shells are close to the measurements and description in the original description and the label, presumably written by Cuming, indicates that these are the three specimens sent to Cuming by Benson, of which two without opercula are syntypes. The third specimen with an operculum being what Benson considered to be ‘*volvulus*’ and not a member of the type series of ‘*malayanus*’. There is a further lot from “Pulo Penang” housed in the University Museum of Zoology Cambridge with original Benson labels including one specimen labelled by Benson as ‘Type’.

***Cyclophorus monachus* (Morelet, 1866)**

http://species-id.net/wiki/Cyclophorus_monachus

Cyclostoma monachus Morelet, 1866: 166.

Cyclophorus monachus – Kobelt 1902: 100. Kobelt 1908: 619.

Type locality. Cochinchina [Saigon, Vietnam].

Type material. Lectotype (design. n.), NHMUK 1893.2.4.499 (Fig. 13B; D=38.2 mm, H=23.7 mm, W=5), paralectotype NHMUK 1893.2.4.500 (1 shell; Fig. 13C; D=35.2 mm, H=22.1 mm, W=5).

Remarks. The original description did not include an illustration and only one set of shell measurements was given. There are two specimens in the NHM collections with an original label stating “Type” and giving the reference of the

original description. The shell that most closely matches with the measurement in the original description and with an “x” written in the aperture is here designated as the lectotype.

***Cyclophorus muspratti* Godwin-Austen & Beddome, 1894**

http://species-id.net/wiki/Cyclophorus_muspratti

Cyclophorus muspratti Godwin-Austen & Beddome, 1894: 506. Kobelt 1902: 101.
Kobelt 1908: 662.

Type locality. Naga Hills, and Maokokehung, Naga Hills [Assam, Arunachal Pradesh and Nagaland, India].

Type material. Holotype NHMUK 1903.7.1.1427/1 from Naga Hills (Fig. 14A; D=48.7 mm, H=36.4 mm, W=5), paratypes NHMUK 1903.7.1.1427/2–4 (3 shells: 2 adults and 1 juvenile; Fig. 14B; D=50.2 mm, H=38.1 mm, W=5; D=47.7 mm, H=38.1 mm, W=5).

Remarks. The original description included two sets of shell measurements (the type and the largest specimen), and Godwin-Austen explicitly stated there to be a unique name-bearing type. The NHM collections contain a lot of four shells from the Godwin-Austen collection (ex. Doherty collection) and have his original handwritten label stating “Type”. The specimen with ‘type’ written on the shell most closely matches with the ‘type’ shell dimensions given in the original description and is here considered to be the holotype, the remaining three shells being paratypes.

***Cyclophorus nagaensis* Godwin-Austen & Beddome, 1894**

http://species-id.net/wiki/Cyclophorus_nagaensis

Cyclophorus nagaensis Godwin-Austen & Beddome, 1894: 507. Kobelt 1902: 101.

Type locality. Naga Hills, near Khonoma and Kigwema, 5000–6000 feet; Maokokehung [Assam, Arunachal Pradesh and Nagaland, India].

Type material. Lectotype (design. n.), NHMUK 1903.7.1.1456/1 from Naga Hills (Fig. 15A; D=45.2 mm, H=35.5 mm, W=5), paralectotypes NHMUK 1903.7.1.1456/2–4 (3 shells; Fig. 15B; D=43.9 mm, H=34.1 mm, W=5; D=44.7 mm, H=35.7 mm, W=5; D=42.3 mm, H=32.7 mm, W=5).

Remarks. The NHM collections contain a lot of four shells from the Godwin-Austen collection (ex. Doherty collection) and have his original handwritten label stating “Type”. The specimen that most closely matches the original description and the measurements given by Godwin-Austen is designated as the lectotype.

***Cyclophorus niahensis* Godwin-Austen, 1889**

http://species-id.net/wiki/Cyclophorus_niahensis

Cyclophorus niahensis Godwin-Austen, 1889: 334, pl. 35, fig. 1. Kobelt 1902: 115.

Type locality. Niah Hills [Sarawak, Malaysia].

Type material. Lectotype (design. n.), NHMUK 1889.12.7.3 (Fig. 15C; D=44.0 mm, H=28.0 mm, W=4), paralectotype NHMUK 1889.12.7.4 (2 shells: 1 adult and 1 juvenile; Fig. 15D; D=41.1 mm, H=24.8 mm, W=4).

Remarks. The use of the term “holotype” in Vermeulen (1999: 144) does not constitute a valid lectotype designation, since there was no explicit indication to a particular specimen (ICZN 1999: Art. 74.5). The specimen which most closely matches the figure in the original description (especially in respect to the position of interrupted growth lines on last whorl) and marked with an “X” on the inside of the aperture is here designated as the lectotype.

***Cyclophorus cochranei ochraceus* Godwin-Austen, 1889**

http://species-id.net/wiki/Cyclophorus_cochranei_ochraceus

Cyclophorus cochranei var. *ochraceus* Godwin-Austen, 1889: 334, 335. Kobelt 1902: 127.

Type locality. Busan Hills [Sarawak, Malaysia].

Type material. Lectotype NHMUK 1889.12.7.6 (Fig. 16A; D=41.7 mm, H=27.4 mm, W=5).

Remarks. The original description clearly stated the taxon was based on two specimens from Busan Hills, and the unique name-bearing type was not stated. However, there is only one remaining specimen from the Godwin-Austen type lot in the NHM collections. Subsequent use of the term “holotype” in Vermeulen (1999: 144) is seemed an unambiguously selected a particular specimen as the name-bearing type. This constitutes a valid lectotype designation (ICZN 1999: Art. 74.5).

***Cyclophorus phlegethon* Godwin-Austen, 1889**

http://species-id.net/wiki/Cyclophorus_phlegethon

Cyclophorus phlegethon Godwin-Austen, 1889: 335, 336. Kobelt 1902: 131.

Type locality. Molu Hills [Sarawak, Malaysia].

Type material. Holotype NHMUK 1998011 (Fig. 16B; D=39.1 mm, H=23.3 mm, W=4).

Remarks. Godwin-Austen clearly stated that this taxon was described based on only one specimen, therefore we recognise this specimen as the holotype fixed by monotypy (ICZN 1999: Art. 73.1.2).

***Cyclophorus picturatus* (Pfeiffer, 1854)**

http://species-id.net/wiki/Cyclophorus_picturatus

Cyclostoma (*Cyclophorus*) *picturatum* Pfeiffer, 1854b [1852]: 62. Pfeiffer 1854a: 347, pl. 45, figs 13, 14.

Cyclophorus picturatus – Reeve 1861: sp. 22. Kobelt 1902: 116. Kobelt 1907: 596.

Type locality. Unknown.

Type material. Lectotype (design. n.) NHMUK 20130082/1 (Fig. 16C, D; D=29.1 mm, H=22.5 mm, W=4½), paralectotypes NHMUK 20130082/2-3 (2 shells; Fig. 16D, D=30.0 mm, H=23.1 mm, W=4½; D=30.4 mm, H=20.8 mm, W=4½).

Remarks. This species was described based on specimens from the Cuming collection. Pfeiffer (1854a: pl. 45, figs 13, 14.) re-published the description and figured this species. The NHM collections contain a lot of three shells from the Cuming collection with original labels in Pfeiffer's handwriting stating the species name. None of these shells exactly match with the illustration in Pfeiffer (1854a). However, the specimen mostly similar to the illustration in Reeve (1861: sp. 22) is illustrated here and is designated as the lectotype.

***Cyclophorus poeciloneurus* Godwin-Austen & Beddome, 1894**

http://species-id.net/wiki/Cyclophorus_poeciloneurus

Cyclophorus poeciloneurus Godwin-Austen & Beddome, 1894: 507, 508. Kobelt 1902: 102. Kobelt 1908: 639.

Type locality. Lahúpa Naga Hills, Manipur, and eastward to the Dihing [India].

Type material. Lectotype (design. n.), NHMUK 1903.7.1.1522/1 from Lahúpa Naga Hills (Fig. 16E; D=31.1 mm, H=24.9 mm, W=5), paralectotype NHMUK 1903.7.1.1522/2 (1 shell; Fig. 16F; D=27.3 mm, H=20.2 mm, W=5).

Remarks. The authors indicated that four lots of specimens were examined in the original description (from the Godwin-Austen, Ogel, Doherty and Beddome collections). In addition, the authors stated "Type" in relation to the specimens from the Godwin-Austen collection, which consist of two shells. The original description did not include an illustration, and only one set of shell measurement was given. The specimen that has a small label stating "Type" glued inside the aperture, and which matched the measurements given in original description is here designated as the lectotype. The paralectotypes from the Ogel, Doherty, and Beddome collections were not found.

***Cyclophorus fulguratus rangunensis* Kobelt, 1908**

http://species-id.net/wiki/Cyclophorus_fulguratus_rangunensis

Cyclophorus fulguratus var. Pfeiffer, 1869: 440, pl. 98, figs 1, 2.

Cyclophorus fulguratus var. *rangunensis* Kobelt, 1908: 647, pl. 93, figs 1, 2. Gude 1921: 61.

Type locality. Inter Thyet-Mio et Rangoon Birmanorum, Pegu [between Thayet District and Yangon in Myanmar, Bago].

Type material. Lectotype (design. n.), NHMUK 20130091/1 (Fig. 17A; D=34.7 mm, H=30.3 mm, W=5), paralectotypes NHMUK 20130091/2-3 (2 shells; Fig. 17B; D=27.4 mm, H=23.4 mm, W=5; D=27.1 mm, H=23.2 mm, W=5).

Remarks. Kobelt (1908) described this species based on Pfeiffer's specimens. Since a range of measurement was given it can be assumed that the taxon was described using more than one specimen. There are three shells in the NHM collections from the Cuming collection with original labels in Pfeiffer's handwriting. One of the specimens matches with figures in Kobelt (1908: pl. 93, figs. 1, 2) and Pfeiffer (1869: pl. 98, figs. 1, 2) and is here designated as the lectotype.

***Cyclophorus eximus rouyeri* Bullen, 1906**

http://species-id.net/wiki/Cyclophorus_eximus_rouyeri

Cyclophorus eximus var. *rouyeri* Bullen, 1906: 343, pl. 25, fig. 5. Kobelt 1908: 680.

Type locality. Mount Singalong [Mount Singgalang, West Sumatra, Indonesia].

Type material. Lectotype (design. n.), NHMUK 1906.1.16.51 (Fig. 17C; D=50.1 mm, H=40.5 mm, W=5), paralectotype NHMUK 20130078 (1 shell; Fig. 17D; D=50.1 mm, H=40.5 mm, W=5).

Remarks. The original description was clearly based on more than one specimen, but only one set of measurements and illustrations were given. There are two shells, from two lots in the NHM collections which are both considered to be part of the original type series. The specimen figured in the original description is here designated as the lectotype.

***Cyclophorus saturnus* Pfeiffer, 1862**

http://species-id.net/wiki/Cyclophorus_saturnus

Cyclophorus saturnus Pfeiffer, 1862: 116, pl. 12, fig. 6. Kobelt 1902: 132.

Type locality. Camboja [Cambodia].

Type material. Lectotype (design. n.), NHMUK 20130119/1 (Fig. 18A; D=63.1 mm, H=46.5 mm, W=5½), paralectotypes NHMUK 20130119/2-3 (2 shells; Fig. 18B; D=57.7 mm, H=43.2 mm, W=5½; D=60.0 mm, H=46.8 mm, W=5½).

Remarks. This species was described based on a specimen collected by M. Mouhot from the Cuming collection, and only one set of shell measurements and one specimen was illustrated in the original description. There are three shells in the NHM collections from the Cuming collection with an original label in Pfeiffer's handwriting stating the taxon name, collector and collection locality. The figured specimen with an "x" written inside the aperture is here designated as the lectotype. The type locality of Cambodia applied to contemporaneous boundaries but Mouhot also collected in an area that now comes within the boundary of southern Vietnam.

Cyclophorus schepmani Laidlaw, 1957

http://species-id.net/wiki/Cyclophorus_schepmani

Cyclophorus schepmani Laidlaw, 1957: 126, 127.

Type locality. Sinabang, Simalur Island, West Sumatra.

Type material. Paratype NHMUK 1957.11.18.7 (1 shell; Fig.19A; D=44.4 mm, H=35.7 mm, W=5 ½).

Remarks. The authors indicated that four lots of specimens were examined in the original description. The original description did not include an illustration, and two set of shell measurement were given. However, the holotype was clearly designated and is housed in the Leiden Museum, Netherlands (now Naturalis Biodiversity Centre). The NHM registration records show that this specimen was purchased from Laidlaw, ex. Dr. Jacobson collection, and the original label states 'paratype'. The locality given by Laidlaw was "2 ex. July; Sinabang" match with the specimen. We therefore consider the single specimen as paratype.

Cyclophorus serratizona Hanley & Theobald, 1876

http://species-id.net/wiki/Cyclophorus_serratizona

Cyclophorus serratizona Hanley & Theobald, 1876: 57, pl. 144, fig. 7. Kobelt 1908: 654. Gude 1921: 77.

Type locality. Upper Salwen [Myanmar].

Type material. Possible syntypes NHMUK 88.12.4.1955 (3 shells, Fig. 19B; D=37.1 mm, H=30.0 mm, W=5; D=39.9 mm, H=30.8 mm, W=5; D=40.7 mm, H=32.9 mm, W=5).

Remarks. This taxon was described based on specimens from the Theobald collection. Coan and Kabat (2012: 326) stated that the types could not be located in either the NHM or the Leeds Museum. We located 3 specimens in the NHM general collection

with a label stating that they were purchased from Theobald, “type figd in C. I.”, but giving Moulmein (currently Mawlamyine), farm (=from?) caves, as the locality, which is at the mouth of the Salween. It seems likely that there is a mix up in the documentation of the locality but we cannot determine if the error is in the locality given in the original description, an error in the labelling with the specimens or if this lot is simply not type material. We therefore treat the material as possible syntypes.

The locality given by Hanley and Theobald was Upper Salween (Salween or currently Thanlwin). However, the material identified as the syntype series carries labels giving Moulmein (currently Mawlamyine), farm (=from?) caves, as the locality, which is at the mouth of the Salween. As the Salween is close to 3,000 km in length and the river originates from the Tibetan Plateau, it is clear that ‘Upper Salween’ is inaccurate. It is conceivable that the intended record was Upper Myanmar but on current evidence we conclude that the Mawlamyine is the type locality.

***Cyclophorus siamensis* (Sowerby I, 1850)**

http://species-id.net/wiki/Cyclophorus_siamensis

Cyclostoma siamense Sowerby I, 1850: 158, pl. 31a, figs 292, 293. Pfeiffer 1854a: 323, pl. 42, figs 5, 6.

Cyclophorus siamensis – Reeve 1861: sp. 19. Kobelt 1902: 132.

Cyclophorus khasiensis Nevill, 1878: 273 (‘new replacement name’).

Type locality. Siam [Thailand].

Type material. Lectotype (design. n.), NHMUK 20130088/1 (Fig. 20A; D=51.2 mm, H=40.0 mm, W=5), paralectotype NHMUK 20130088/2 (1 shell; Fig. 20B; D=49.8 mm, H=39.5 mm, W=5).

Remarks. The original description as well as those in Pfeiffer (1854a: 323) are particularly accurate, both showing the dark banding pattern and varix on the last whorl, and both figures appear to be from the same specimen. The NHM collections contain two shells from the Cuming collection with original labels stated the taxon name, type locality and “f. 292, 293”. The specimen which corresponds to the illustrations in Sowerby I (1850) and Pfeiffer (1854a) is here designated as the lectotype.

Nevill (1878: 273) stated that *Cyclostoma siamensis* Sowerby I, 1850 occur in Khasi Hills, India not in Siam. Nevill considered this is an inappropriate taxon name, and *Cyclophorus khasiensis* Nevill, 1878 was nominated as a new replacement name based on specimens from the Godwin-Austen collection. This is however an unjustified replacement name, and therefore a junior objective synonym of *Cyclostoma siamensis* Sowerby I, 1850 (ICZN 1999: Arts 18, 72.7). The specimens of *Cyclophorus khasiensis* in the Godwin-Austen collection have no nomenclatural status.

It should be noted that Kobelt (1902) attributed the date of publication of this species in error as “1843”. For the correct dates of publication for “Thesaurus Conchyliorum” see Petit (2009: 32).

***Cyclophorus spironema* (Pfeiffer, 1855)**

http://species-id.net/wiki/Cyclophorus_spironema

Cyclostoma (*Cyclophorus*) *spironema* Pfeiffer, 1855a [1854]: 127.

Cyclophorus spironema – Kobelt 1902: 104.

Type locality. India.

Type material. Lectotypes (design. n.), NHMUK 20130083/1 (Fig. 21A; D=27.9 mm, H=19.8 mm, W=4), paralectotypes NHMUK 20130083/2-3 (2 shells; Fig. 21B; D=26.8 mm, H=21.4 mm, W=4; D=28.2 mm, H=20.9 mm, W=4).

Remarks. This species was described based on specimens from the Cuming collection. The NHM collections contain three shells from the Cuming collection with an original label in Pfeiffer's handwriting giving the taxon name and collection locality. The specimen figured in Gude (1921: 55, 56, fig. 13) does not constitute a lectotype designation; as Gude did not select a particular syntype to be the unique name-bearing type (ICZN 1999: Art. 74.3). We here designate the specimen figured in Gude (1921: fig. 13) as the lectotype.

***Cyclophorus subblaevigatus* Blanford, 1869**

http://species-id.net/wiki/Cyclophorus_subblaevigatus

Cyclophorus subblaevigatus Blanford, 1869: 446, 447. Hanley and Theobald 1870: 16, pl. 34, fig. 7. Kobelt 1902: 133.

Type locality. haud procul a Bhamo, ad ripas fluminis Iravadi [not far from the Bhamo, on the banks of the Iravadi River, Myanmar].

Type material. Lectotype (design. n.), NHMUK 196550 (Fig. 21C; D=46.1 mm, H=30.8 mm, W=5).

Remarks. The term “nonnunquam” (“sometimes”) in the original description of shell shape appears to imply that this taxon was based on more than one specimen although only one set of measurements was given in the original description. The use of “the type” in Hanley and Theobald (1870: 16) may not constitute a valid lectotype designation because a label stating that it is the figured specimen is not in Hanley or Theobald's hand and it is not clear if only one specimen was available to Hanley and Theobald. We therefore treat “the type” attribution as an invalid, inadvertent lectotype designation (ICZN 1999: Art. 74.5). The single specimen in the NHM from the Blanford collection and figured in Hanley and Theobald (1870: pl. 34, fig. 7), is here designated as the lectotype.

***Cyclophorus taeniatus* (Pfeiffer, 1855)**

http://species-id.net/wiki/Cyclophorus_taeniatus

Cyclostoma (*Cyclophorus*) *taeniatum* Pfeiffer, 1855b [1854]: 301.

Cyclophorus taeniatus – Reeve 1861: sp. 39. Kobelt 1902: 134.

Type locality. Sumatra.

Type material. Lectotype (design. n.), NHMUK 20130120 (Fig. 21D; D=28.1 mm, H=23.6 mm, W=5).

Remarks. This species was described based on specimens from the Cuming collection. The NHM collections contain a single specimen from the Cuming collection with an original label in Pfeiffer's handwriting giving the taxon name and collection locality. This single specimen closely matches with the measurements given in the original description and the illustration in Reeve (1861: sp. 39) and is here designated as the lectotype.

***Cyclophorus talboti* Godwin-Austen, 1889**

http://species-id.net/wiki/Cyclophorus_talboti

Cyclophorus talboti Godwin-Austen, 1889: 335. Kobelt 1902: 119.

Type locality. Busan Hills [Sarawak, Malaysia].

Type material. Lectotype, NHMUK 1889.12.7.7 (Fig. 21E; D=40.1 mm, H=27.5 mm, W=5)

Remarks. Godwin-Austen stated that this taxon was named after Captain Talbot and based on specimens from the collection of A. Everett. The NHM collections contain a lot of three specimens mounted on a single specimen board. The specimen labelled 1889.12.7.7 is marked with the word type, and the original description details. The two other specimens are from the W. Jeakes Esq. (NHMUK 1859.3.30.12) and C. Hose Esq. (1893.3.10.3) collections and have no associated locality data and are therefore excluded from the type series. The use of the term "holotype" in Vermeulen (1999: 144) is an inadvertent lectotype designation since a particular shell was selected to be the unique name-bearing type (ICZN 1999: Art. 74.5).

***Cyclophorus tigrinus* (Sowerby I, 1843)**

http://species-id.net/wiki/Cyclophorus_tigrinus

Cyclostoma tigrinum Sowerby I, 1843a: 30. Sowerby I 1843c: 126, pl. 29, figs 201–204.

Pfeiffer 1848: 61, pl. 8, figs 13–16.

Cyclophorus tigrinus – Kobelt 1907: 578.

Type locality. Unknown.

Type material. Lectotype (design. n.), NHMUK 20110231/1 (Fig. 22A; D=32.1 mm, H=28.2 mm, W=6), paralectotypes NHMUK 20110231/2-3 (2 shells; Fig. 22B; D=28.0 mm, H=25.5 mm, W=6; D=30.4 mm, H=26.2 mm, W=6).

Remarks. The original description of this species included seven varieties indicated with “var. a” to “var. g” from the Cuming Collection. Latin and English descriptions associated with illustrations were then published in the “Thesaurus Conchyliorum” (Sowerby I 1843c). None of the subsequent authors recognized or used these seven varietal names. Two further works provided illustrations of the species from the Cuming coll. (Pfeiffer 1848: pl. 8, figs 13–16; pl. 16, figs 17–20; Reeve 1861: sp. 25a, b; 8 fig. 30). These subsequently published illustrations match the specimens in the Cuming collection labelled as “var. a”. Therefore we believe this implies that “var. a” is the type series of *Cyclostoma tigrinum* s.s. and the specimens labelled as “var. b” are distinct variants and are therefore excluded from the type series of this nominal species (ICZN 1999: Art. 72.4.1). The specimen of “var. a” illustrated by Sowerby I (1843c: pl. 29, figs 201, 202) is here designated as the lectotype.

Measurements of specimens in “var. b” are given for future reference:

“var. b.” NHMUK 20110232 from Guimaras Island [Philippines] (3 shells; D=30.5 mm, H=26.5 mm, W=6; D=28.0 mm, H=26.6 mm, W=6; D=27.2 mm, H=22.3 mm, W=6).

***Cyclophorus tuba* (Sowerby I, 1842)**

http://species-id.net/wiki/Cyclophorus_tuba

Cyclostoma tuba Sowerby I, 1842: 83. Sowerby I 1843c: 122, pl. 27, figs 129, 130.

Pfeiffer 1849: 169, pl. 23, figs 10, 11.

Cyclophorus tuba – Reeve 1861: sp. 9. Kobelt 1902: 134.

Type locality. prope Montem Ophir, Malacca [Gunung Ledang, Johor, Malaysia].

Type material. Lectotype (design. n.), NHMUK 20120064/1 (Fig. 22C; D=51.1 mm, H=35.7 mm, W=5), paralectotype NHMUK 20120064/2 (1 shell; Fig. 22D; D=48.1 mm, H=33.4 mm, W=5).

Remarks. The original description of this species included two un-named varieties from the Cuming Collection. The NHM collection contain two lots from the Cuming collection with the original labels giving the taxon name, type locality and varietal names stated as “var. a” and “var. b”. Latin and English descriptions associated with illustrations were then published in the “Thesaurus Conchyliorum” (Sowerby I 1843c). Two further works provided illustrations of the species from Cuming coll. (Pfeiffer 1849: 169, pl. 23, figs 10, 11; Reeve 1861: sp. 9). These subsequently published illustrations match specimens in the Cuming collection labelled as “var. a”. We consider that this implies that “var. a” is the type series of *Cyclostoma tuba* s.s. and the specimens labelled as “var. b” are distinct variants and are therefore excluded from the type series

(ICZN 1999: Art. 72.4.1). The specimen of “var. a” illustrated by Sowerby I (1843c: 122, pl. 27, figs 129, 130) is here designated as the lectotype.

Measurements of specimens in “var. b” are given for future reference:

“var. b.” NHMUK 20120065 from Mountain Ophir, Malacca [Malaysia] (3 shells; D=50.4 mm, H=33.8 mm, W=5; D=50.1 mm, H=35.5 mm, W=5; D=48.1 mm, H=34.0 mm, W=5).

***Cyclophorus turgidus* (Pfeiffer, 1851)**

http://species-id.net/wiki/Cyclophorus_turgidus

Cyclostoma turgidum Pfeiffer, 1851: 139, 140 (‘new replacement name’). Pfeiffer 1853a: 257, pl. 35, fig. 15, 16.

Cyclostoma crassum Pfeiffer, 1853b [1851: 242] (non C.B. Adams 1851).

Cyclophorus turgidus – Reeve 1861: sp. 43.

Cyclophorus crassus – Kobelt 1902: 136, 137.

Type locality. Liew Kiew [Ryukyu Islands, Japan].

Type material. Lectotype (design. n.), NHMUK 20040591/1 (Fig. 23A; D=27.1 mm, H=23.1 mm, W=5), paralectotypes NHMUK 20040591/2-3 (2 shells; Fig. 23B; D=25.9 mm, H=21.3 mm, W=5; D=25.2 mm, H=20.5 mm, mm, W=5).

Remarks. The name *Cyclostoma turgidum* Pfeiffer, 1851 was presented as a replacement name for *Cyclostoma crassum* Pfeiffer, 1853, a junior homonym. However since the “*crassum*” description was not published until 1853 (in the Proceedings of the Zoological Society for 1851 volume, see Duncan 1937) *Cyclostoma turgidum* is the valid original description. This taxon was described and illustrated based on specimens from the Cuming collection. The NHM collections contain two lots from the Cuming collection that have original labels in Pfeiffer’s handwriting with a striking-through of the taxon name “*crassum*”, replaced with “*turgidum*”. One lot of 3 specimens, NHMUK 20040591, has the collection locality “Liew Kiew” which matches with that given in the original description. The specimen figured in Pfeiffer (1853a: pl. 35, figs 15, 16) which matches with the measurements given in the original description is here designated as the lectotype. The second lot of three shells, NHMUK 20040590, has the collection locality “Ibyat, Bashee Islands” which corresponds to “var. minor in insula Ibyat (Bashee group)” from the Pfeiffer’s (1853b) “*crassum*” description and is excluded from the type series of this nominal species (ICZN 1999: Art. 72.4.1).

Measurements of the specimens “var. minor” are given for future reference:

“var. minor” NHMUK 20040590 from Ibyat, Bashee Island [Batan, Island, Philippines] (3 shells; D=20.5 mm, H=16.8 mm, W=5; D=21.0 mm, H=17.9 mm, W=5; D=20.8 mm, H=16.3 mm, W=5).

***Cyclophorus validus* (Sowerby I, 1842)**

http://species-id.net/wiki/Cyclophorus_validus

Cyclostoma validum Sowerby I, 1842: 82. Sowerby I 1843c: 123, pl. 27, figs 132, 133.

Pfeiffer 1848: 89, pl. 11, figs 9, 10.

Cyclophorus validus – Reeve 1861: sp. 23c, d. Kobelt 1902: 120. Kobelt 1908: 581.

Type locality. Island of Leyte, island of Luçon, island of Samar and island of Mindanao, Philippines.

Type material. Lectotype (design. n.), NHMUK 20110280/1 from island of Leyte (Fig. 23C; D=47.9 mm, H=40.4 mm, W=5), paralectotypes NHMUK 20110280/2-3 (2 shells; Fig. 23D; D=46.7 mm, H=39.9 mm, W=5; D=44.0 mm, H=37.6 mm, W=5).

Remarks. The original description of this species included four varieties indicated “var. a” to “var. d”, without illustration from the Cuming Collection. Subsequent authors (including Sowerby I 1843b) did not recognise or use these varietal names. The NHM collections contain four lots of Cuming collection material with original labels giving the taxon and varietal names “var. a” to “var. d”. The description and illustration in Sowerby I (1843b) match the specimens in the Cuming collection labelled as “var. a”. We consider that this implies that “var. a” is the type series of *Cyclostoma validum* s.s. and the specimens labelled as “var. b”, “var. c” and “var. d” are distinct variants and are therefore excluded from the type series (ICZN 1999: Art. 72.4.1). The specimen of “var. a” illustrated by Sowerby I (1843c: pl. 27, figs 132, 133), is here designated as the lectotype.

Measurements of specimens in “var. b” to “var. d.” are given for future reference:

“var. b.” NHMUK 20110281 from Tayabas Province, Luzon [Philippines] (3 shells; D=39.2 mm, H=35.8 mm, W=5; D=38.2 mm, H=33.9 mm, W=5; D=36.8 mm, H=34.2 mm, mm, W=5).

“var. c.” NHMUK 20110282 from Catbalonga and Basay, Samar Island [Philippines] (3 shells; D=43.5 mm, H=34.8 mm, W=5; D=43.8 mm, H=34.6 mm, W=5; D=44.5 mm, H=34.9 mm, W=5).

“var. d.” NHMUK 20110283 from Cagayan, Misamis Province, Mindanao Island, Luzon [Philippines] (3 shells; D=35.6 mm, H=28.4 mm, W=5; D=33.1 mm, H=26.1 mm, W=5; D=32.7 mm, H=25.4 mm, mm, W=5).

Plates

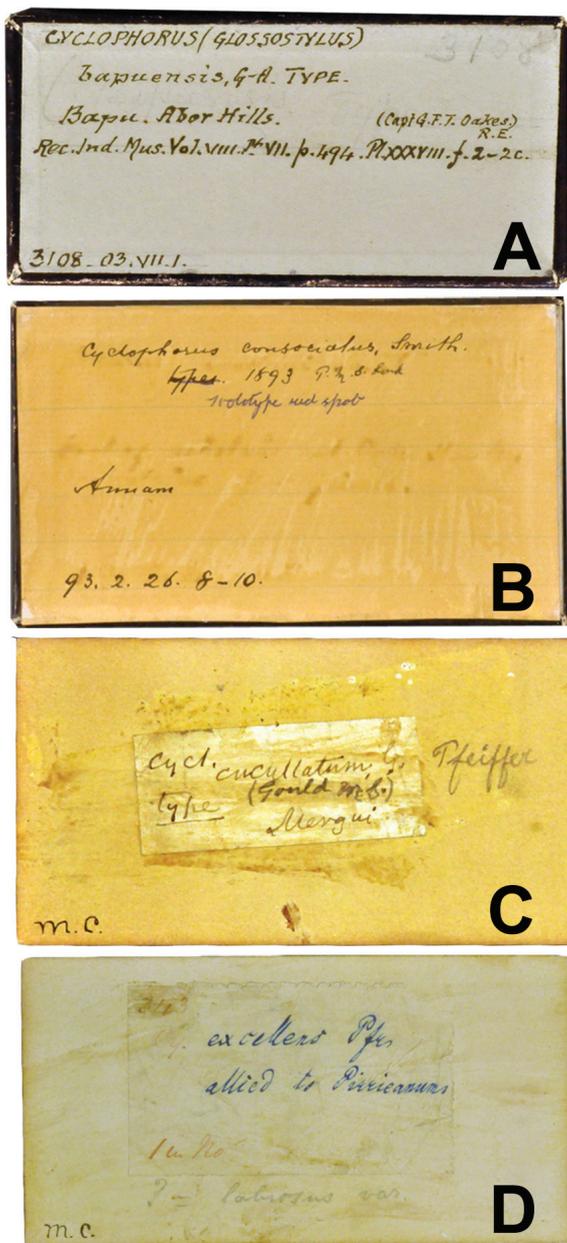


Figure 1. **A** Original labels of *Cyclophorus bapuensis* bearing the author's, H.H. Godwin-Austen handwriting **B** Original labels of *Cyclophorus consociatus* bearing the author's, E.A. Smith handwriting. Note that the strikethrough on the "type" and "Holotype red spot" with blue pen are possibly added later by the NHM assistant **C** The original label of *Cyclophorus cucullatus* marked with "Type" is not frequently occurred in Cuming collection, which the possibly indicates specimen received from A.A. Gould **D** The small glued-label written with blue ink on "excellens Pfr" and "allied to pirreanum" are Pfeiffer's handwritten.

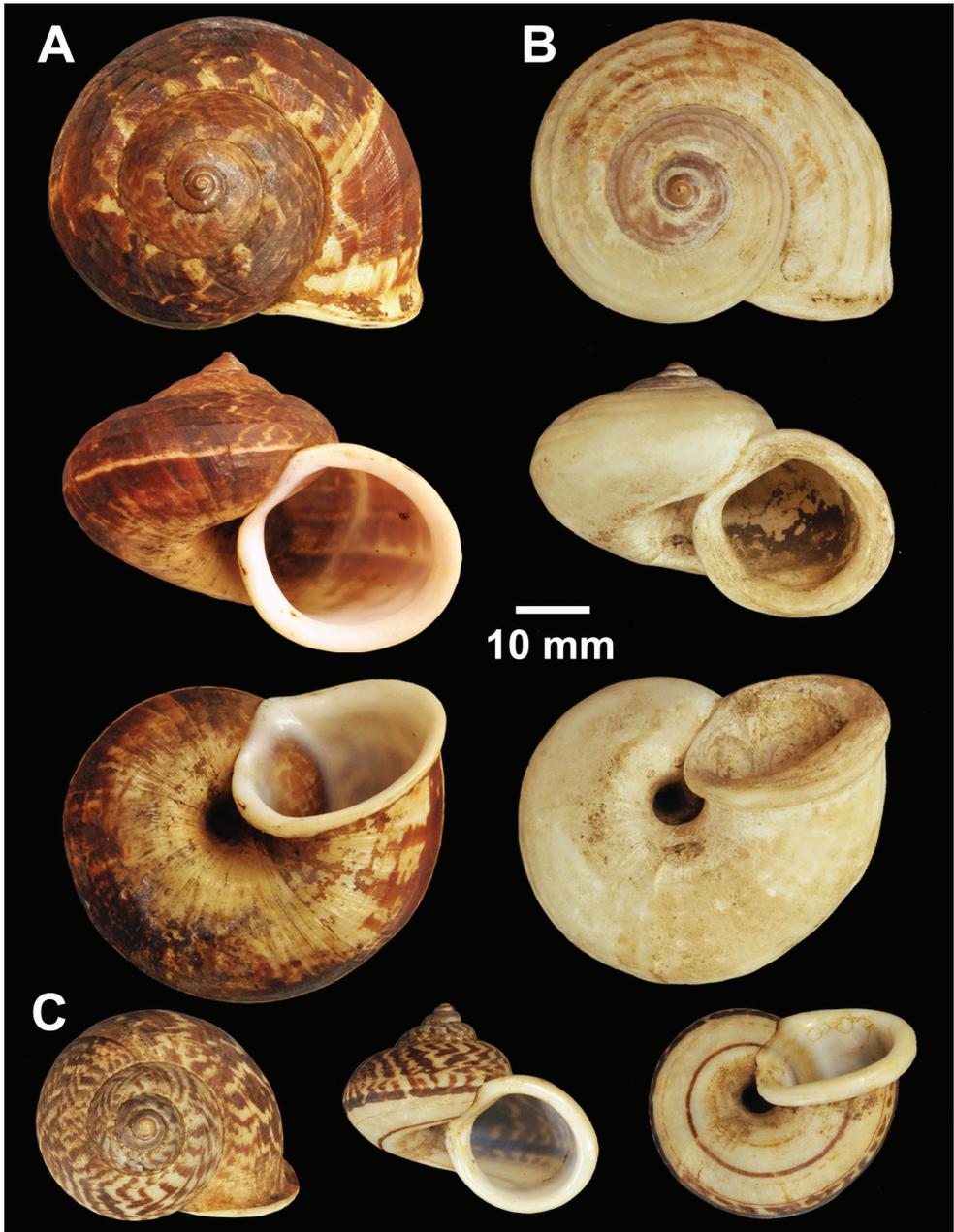


Figure 2. Types of *Cyclophorus* species. **A, B** *Cyclophorus aborensis* Godwin-Austen, 1915 **A** lectotype NHMUK 1903.7.1.3051 and **B** paralectotype NHMUK 1903.7.1.3048 **C** *Cyclophorus affinis* Theobald, 1858, lectotype NHMUK 1903.7.1.1454.

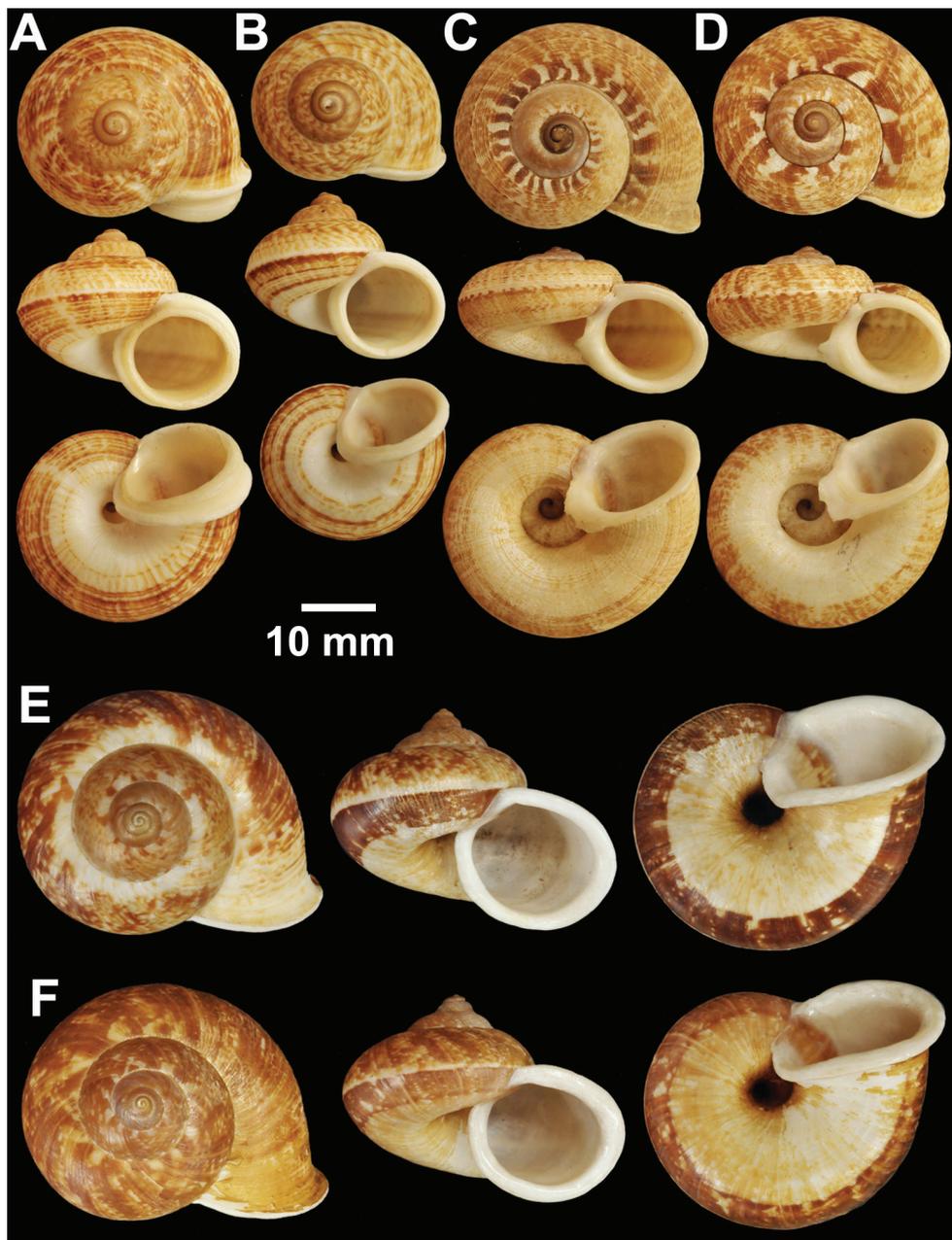


Figure 3. Types of *Cyclophorus* species. **A, B** *Cyclophorus amoenus* (Pfeiffer, 1854) **A** lectotype NHMUK 20130113/1, and **B** paralectotype NHMUK 20130113/2 **C, D** *Cyclophorus appendiculatus* (Pfeiffer, 1854) **C** lectotype NHMUK 20130079/1, and **D** paralectotype NHMUK 20130079/2-3 **E, F** *Cyclophorus aquilus* (Sowerby I, 1843) **E** lectotype NHMUK 20110225/1, and **F** paralectotype NHMUK 2011225/2-3.

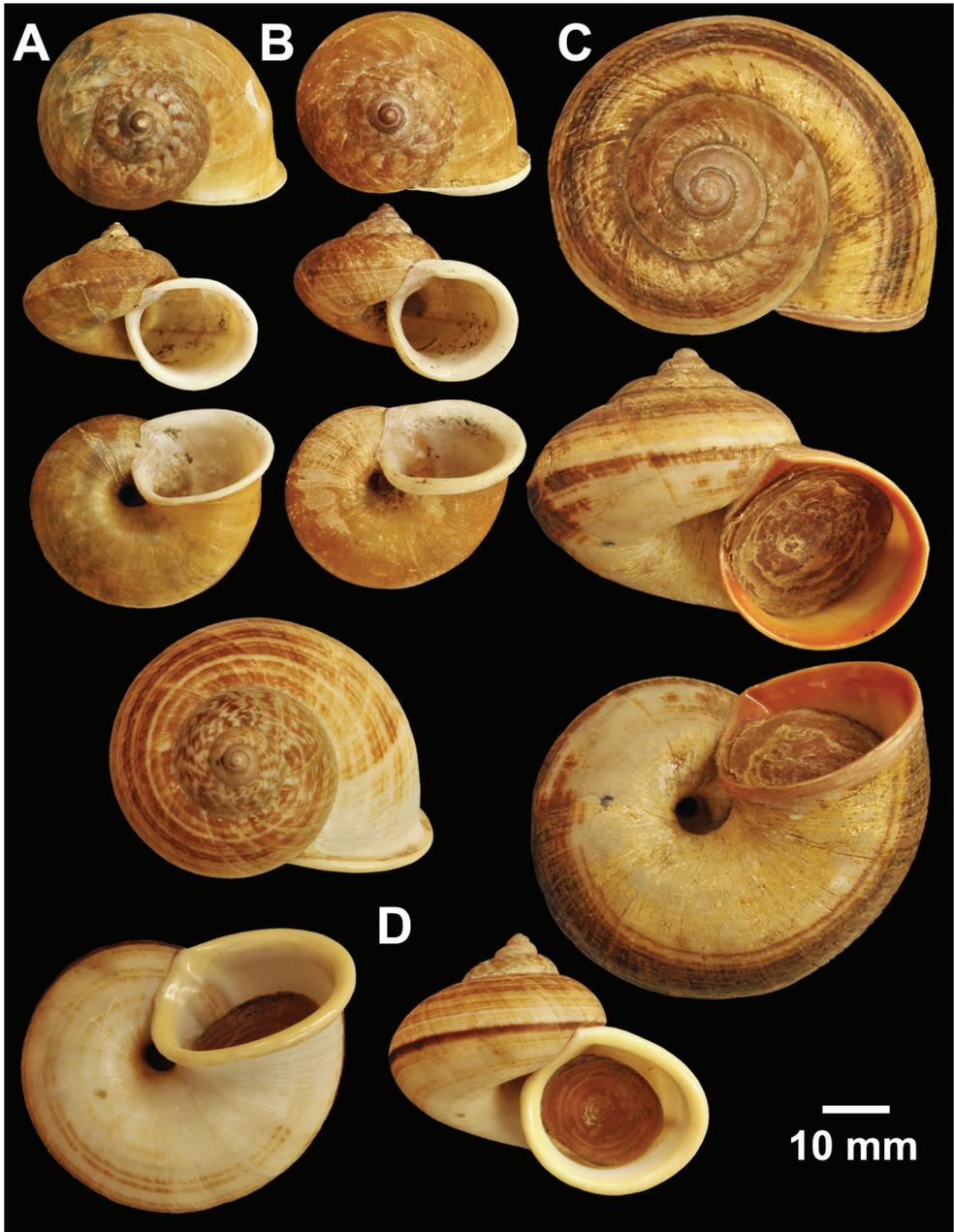


Figure 4. Types of *Cyclophorus* species. **A, B** *Cyclophorus bapuensis* Godwin-Austen, 1915 **A** lectotype NHMUK 1903.7.1.3108/1, and **B** paralectotype NHMUK 1903.7.1.3108/2-3 **C** *Cyclophorus beddomeanus* Preston, 1914 lectotype NHMUK 1936.4.15.22 **D** *Cyclophorus bensoni* (Pfeiffer, 1854) lectotype NHMUK 20130115.

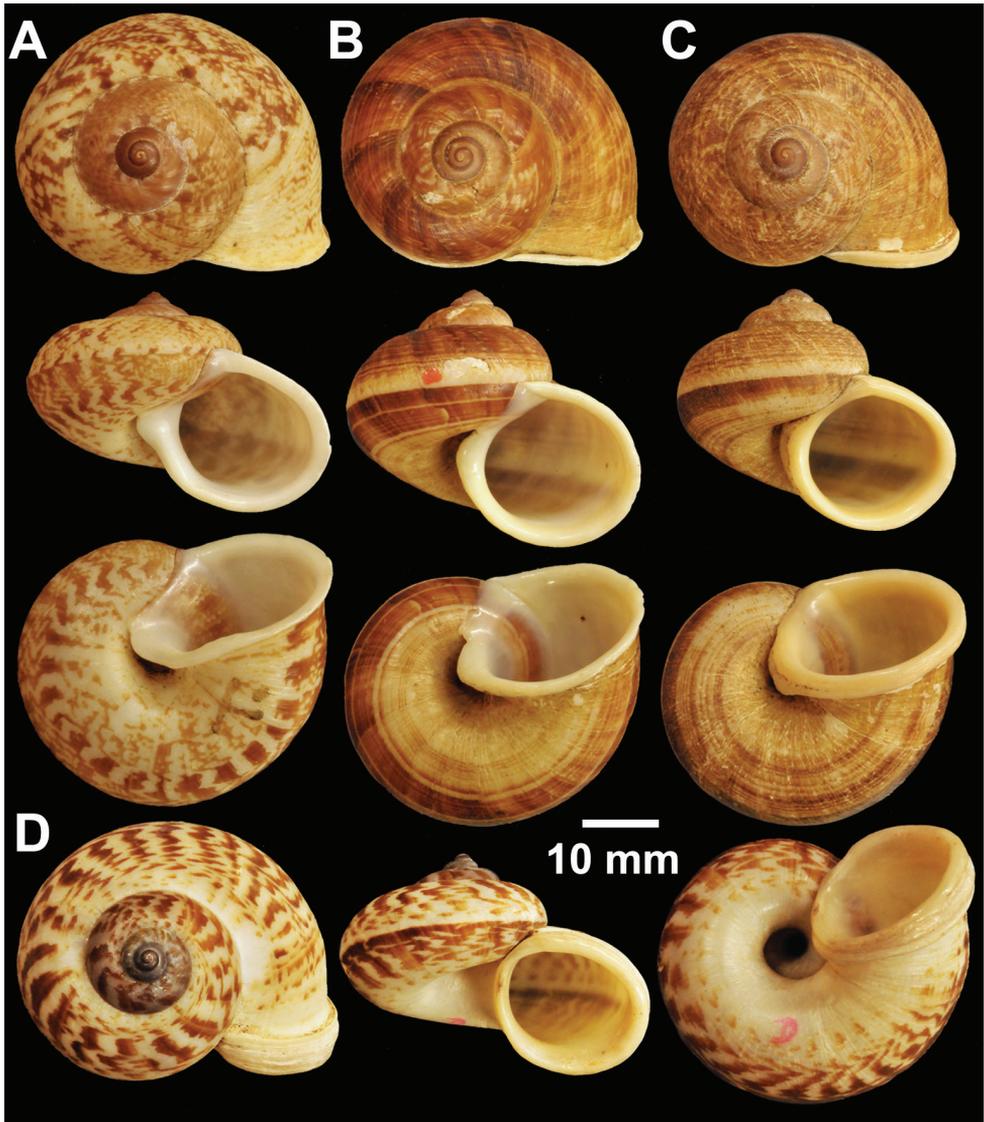


Figure 5. Types of *Cyclophorus* species. **A** *Cyclophorus cochranei* Godwin-Austen, 1889 lectotype NHMUK 1889.12.7.5 **B, C** *Cyclophorus consociatus* Smith, 1893 **B** lectotype NHMUK 1893.2.26.8, and **C** paralectotype NHMUK 1893.2.26.9-10 **D** *Cyclophorus crassalabella* Godwin-Austen, 1888 lectotype NHMUK 1911.6.10.8.

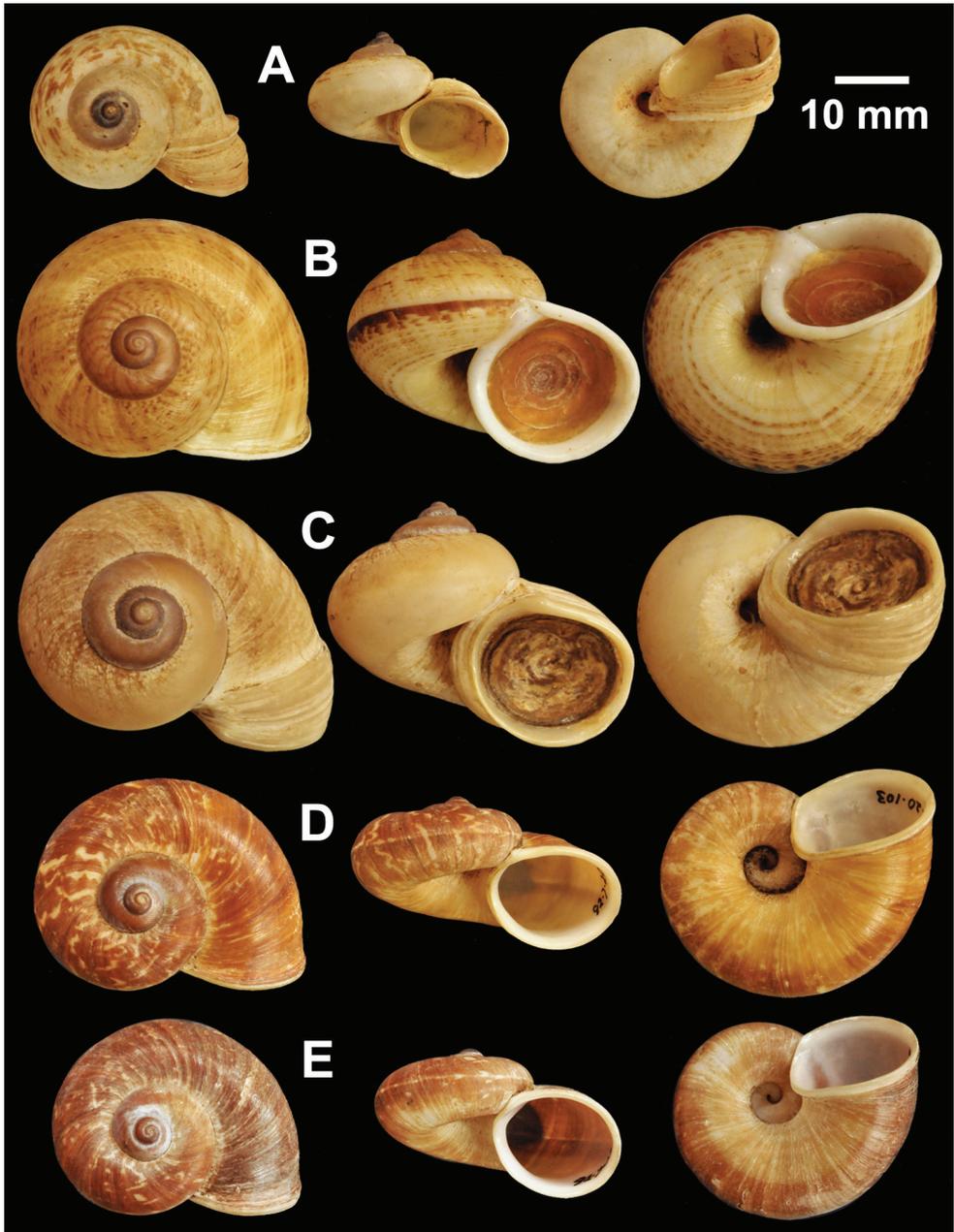


Figure 6. Types of *Cyclophorus* species. **A** *Cyclophorus cucullatus* (Gould, 1856) paralectotypes NHMUK 20130116 **B, C** *Cyclophorus eudeli* Smith, 1893 **B** lectotype NHMUK 1893.2.26.5, and **C** paralectotype NHMUK 1893.2.26.6-7 **D, E** *Cyclophorus everetti* Smith, 1892 **D** lectotype NHMUK 1892.7.20.103, and **E** paralectotype NHMUK 1892.7.23.1-2.

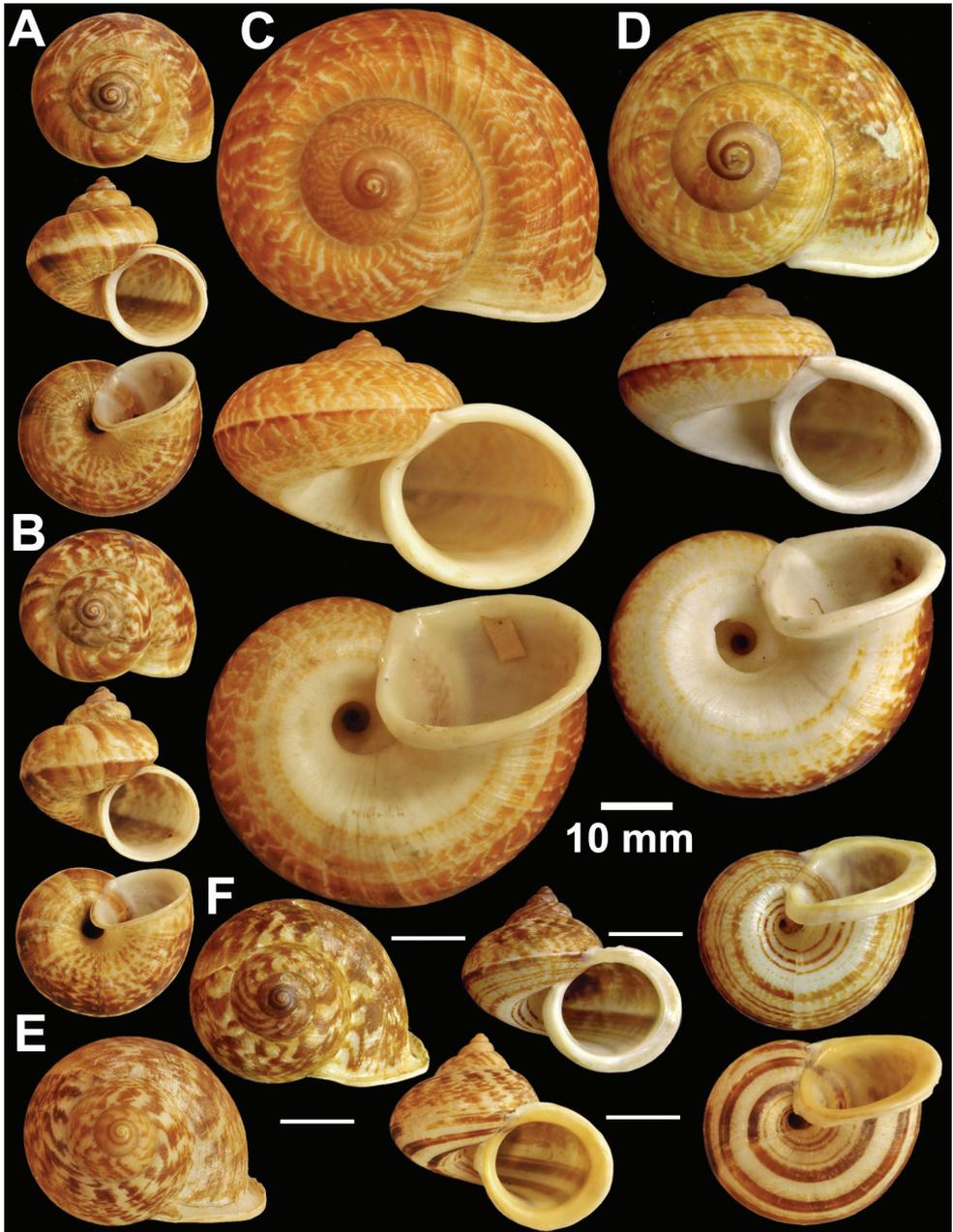


Figure 7. Types of *Cyclophorus* species. **A, B** *Cyclophorus exaltatus* (Pfeiffer, 1855) **A** lectotype NHMUK 1980041/1, and **B** paralectotype NHMUK 1980041/2-3 **C, D** *Cyclophorus excellens* (Pfeiffer, 1855) **C** lectotype NHMUK 20130084/1, and **D** paralectotype NHMUK 20130084/2 **E, F** *Cyclophorus expansus* (Pfeiffer, 1853) **E** lectotype NHMUK 20130086/1, and **F** paralectotype NHMUK 20130086/2-3.

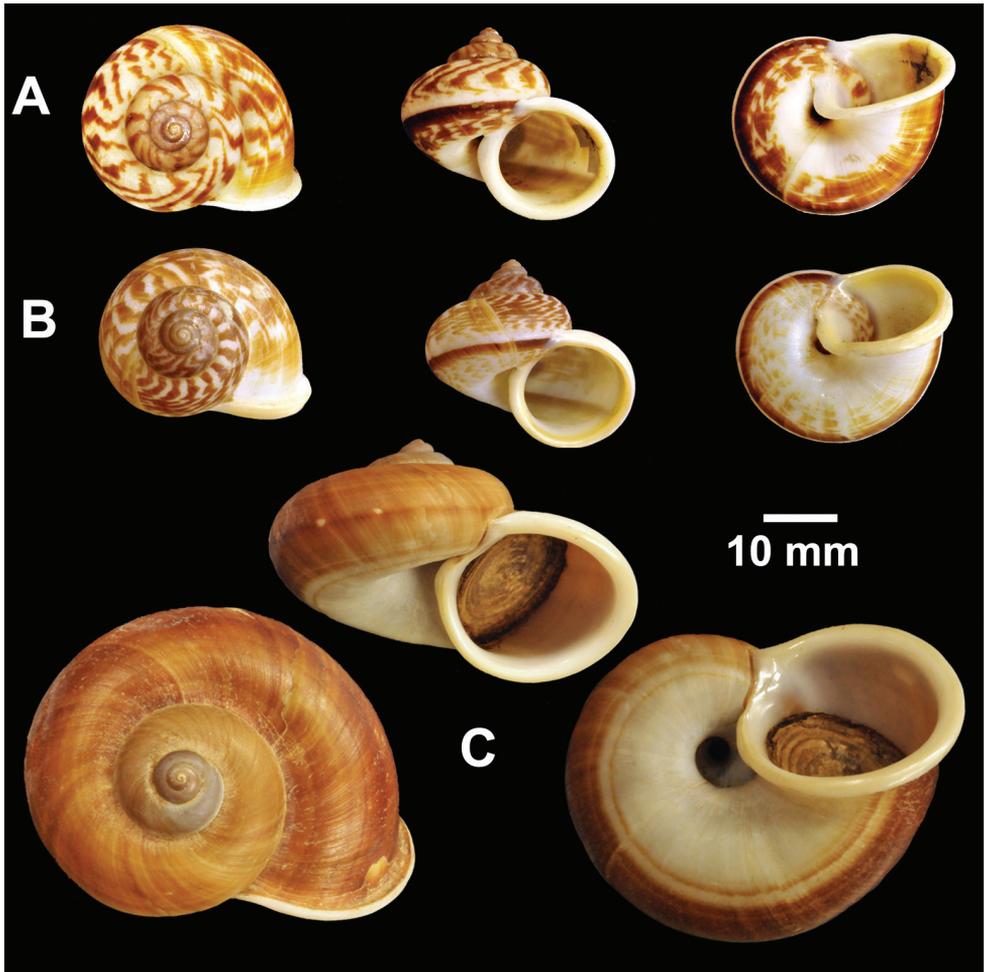


Figure 8. Types of *Cyclophorus* species. **A, B** *Cyclophorus fulguratus* (Pfeiffer, 1854) **A** lectotype NHMUK 20130117/1, and **B** paralectotype NHMUK 20130117/2-3 **C** *Cyclophorus fultoni* Godwin-Austen & Beddome, 1894, lectotype NHMUK 1894.6.20.1.



Figure 9. Types of *Cyclophorus* species. **A, B** *Cyclophorus fuscicolor* Godwin-Austen, 1876 **A** lectotype NHMUK 1903.7.1.1452/1, and **B** paralectotype NHMUK 1903.7.1.1452/2.

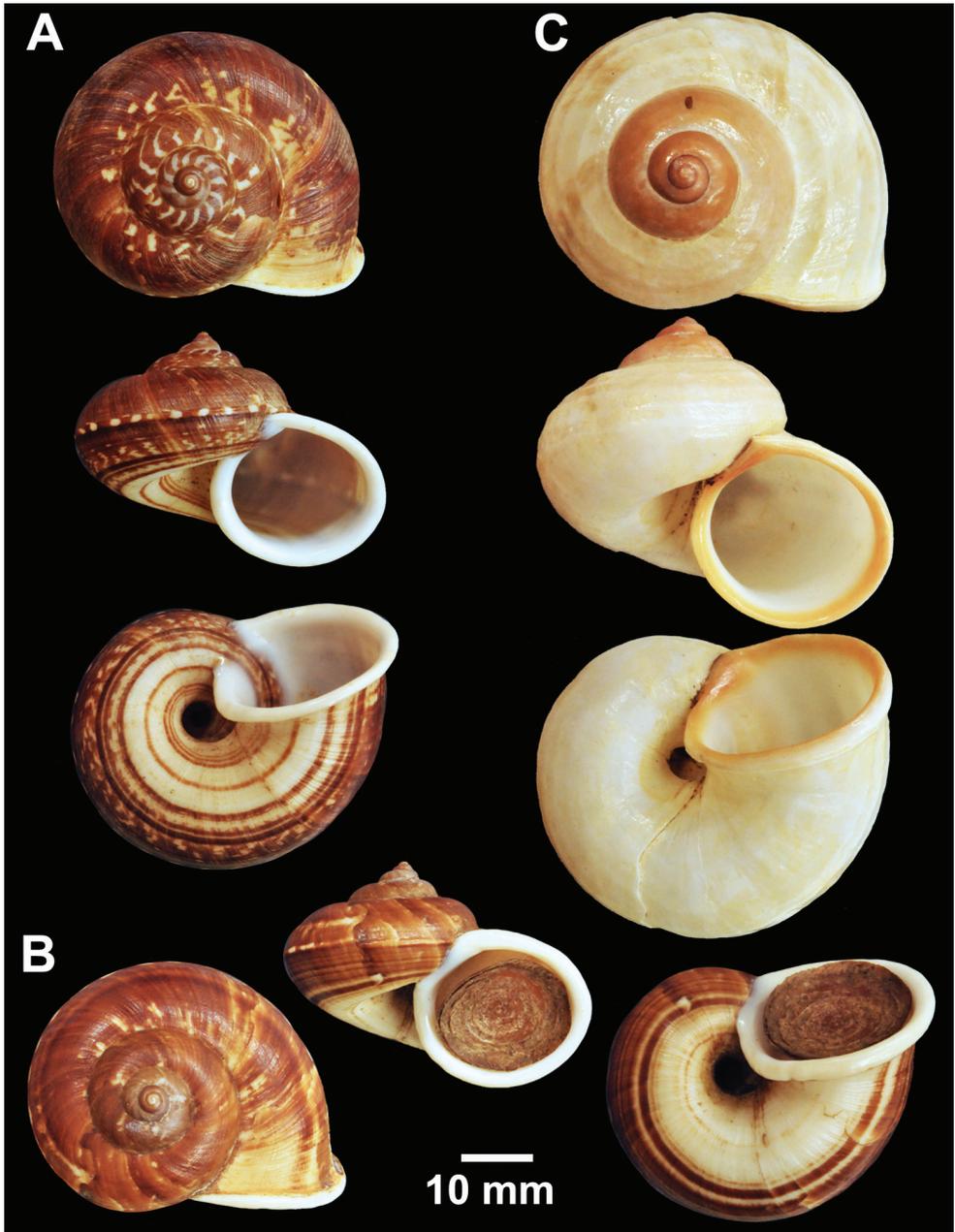


Figure 10. Types of *Cyclophorus* species. **A, B** *Cyclophorus haughtoni* Theobald, 1858 **A** lectotype NHMUK 1888.12.4.1953, and **B** paralectotypes NHMUK 1888.12.4.1954 **C** *Cyclophorus himalayanus* (Pfeiffer, 1853), lectotype NHMUK 20130118.

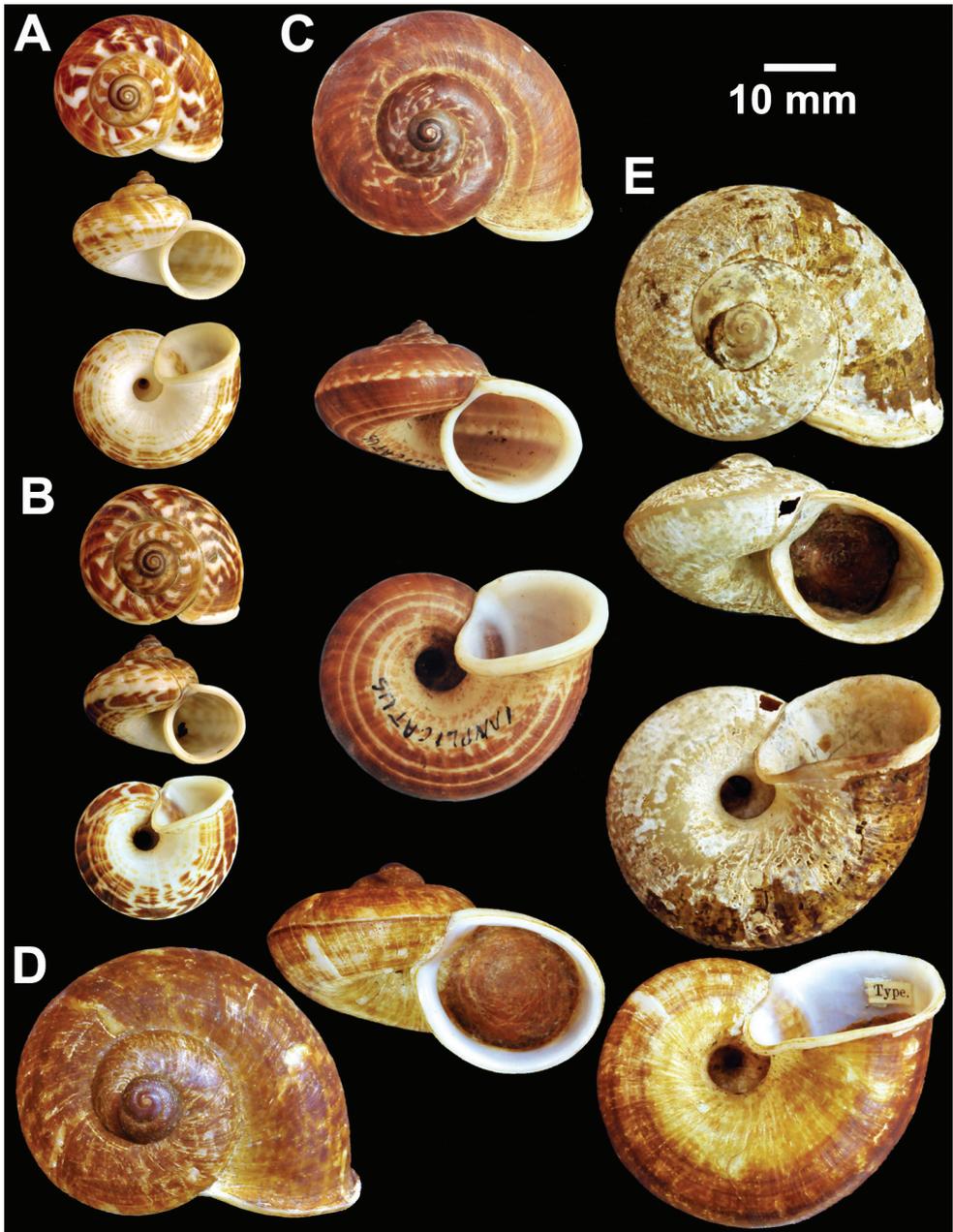


Figure 11. Types of *Cyclophorus* species. **A, B** *Cyclophorus ibyatensis* (Pfeiffer, 1854) **A** lectotype NHMUK 20130081/1, and **B** paralectotype NHMUK 20130081/2 **C** *Cyclophorus implicatus* Bavay and Dautzenberg, 1908, paralectotype NHMUK 20130087 **D, E** *Cyclophorus kinabaluensis* Smith, 1895 **D** lectotype NHMUK 1894.7.20.38, and **E** paralectotype NHMUK 1893.6.8.31.

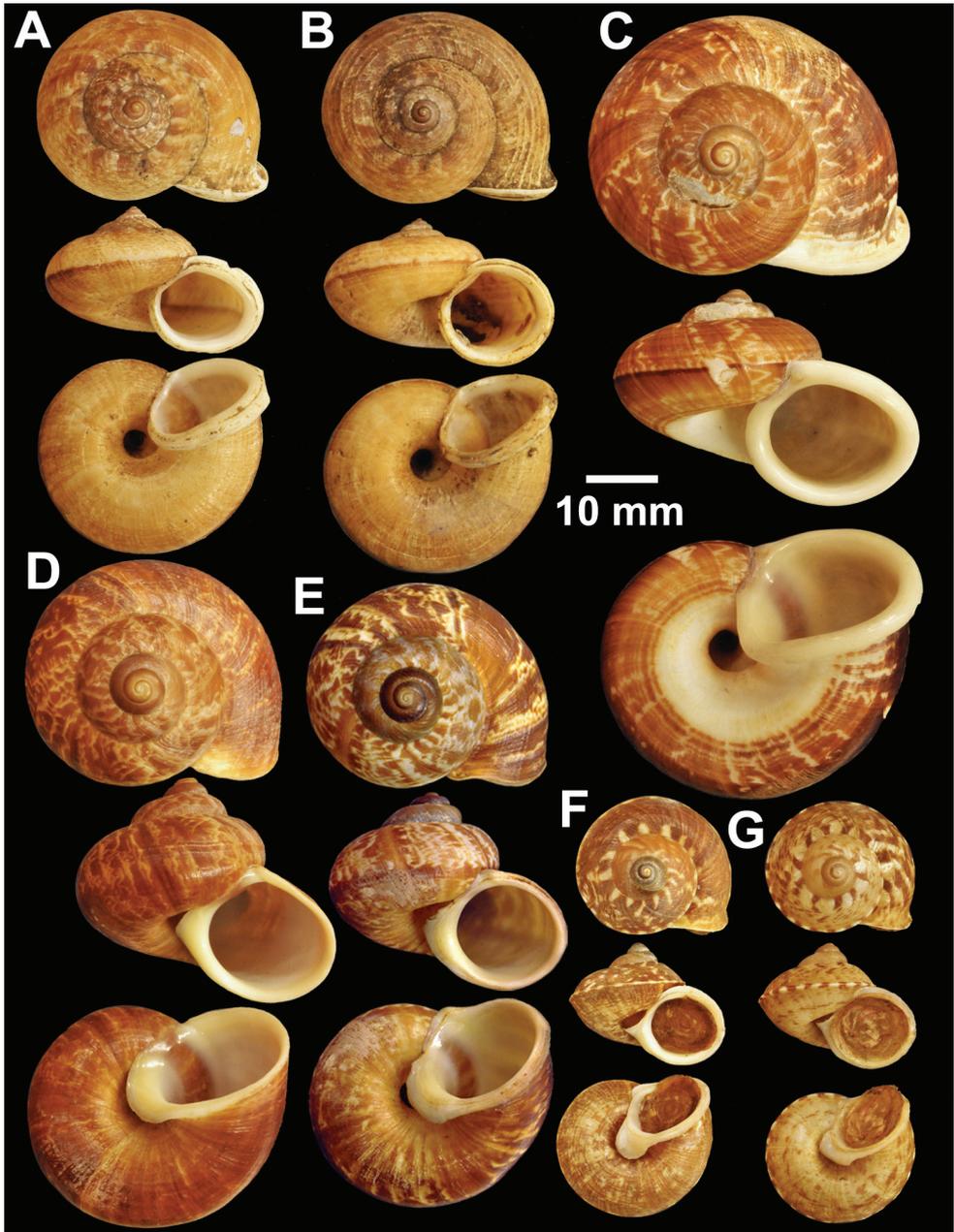


Figure 12. Types of *Cyclophorus* species. **A, B** *Cyclophorus koboensis* Godwin-Austen, 1915 **A** lectotype NHMUK 1903.7.1.3579/1, and **B** paralectotype NHMUK 1903.7.1.3579/2-4 **C** *Cyclophorus labiosus* (Pfeiffer, 1854), lectotype NHMUK 20130080 **D, E** *Cyclophorus linguiferus* (Sowerby I, 1843) **D** lectotype NHMUK 20110269/1, and **E** paralectotype NHMUK 20110269/2-3 **F, G** *Cyclophorus lingulatus* (Sowerby I, 1843) **F** lectotype NHMUK 20110272/1, and **G** paralectotype NHMUK 20110272/2-3.

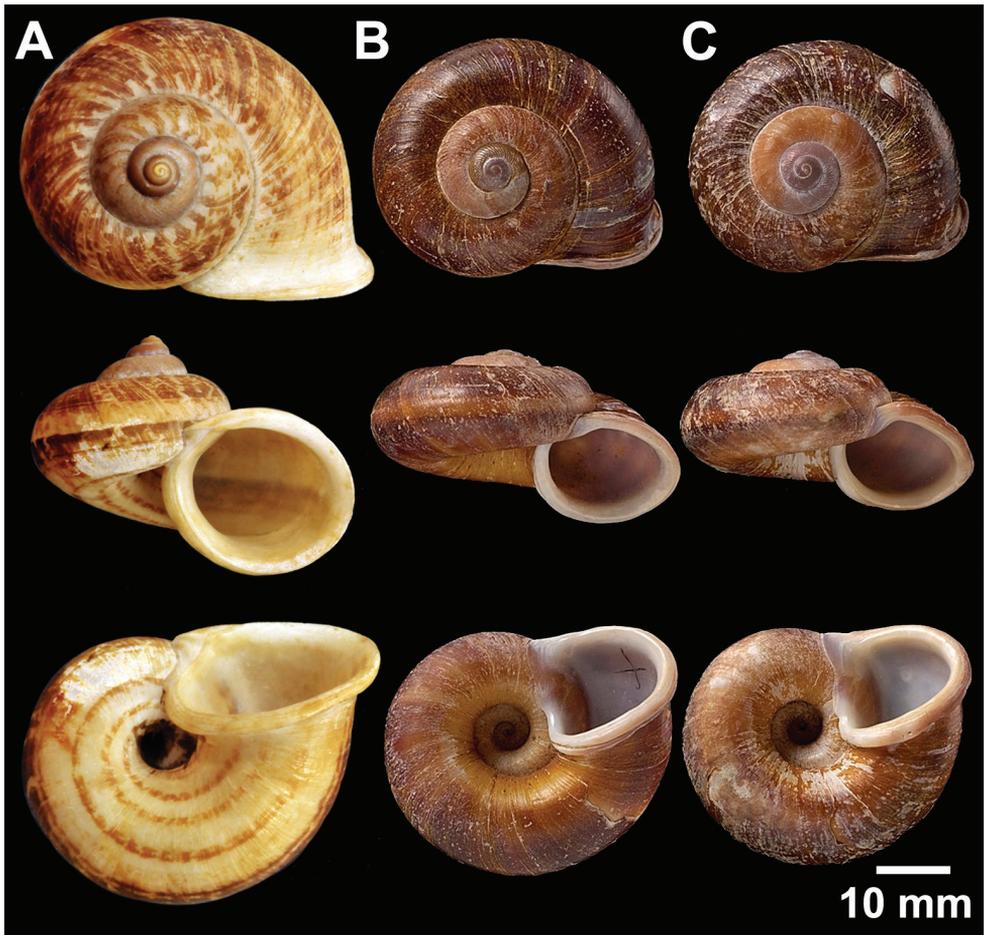


Figure 13. Types of *Cyclophorus* species. **A** *Cyclophorus malayanus* (Benson, 1852), syntype NHMUK 20130089 **B, C** *Cyclophorus monachus* (Morelet, 1866) **B** lectotype NHMUK 1893.2.4.499, and **C** paralectotype NHMUK 1893.2.4.500.

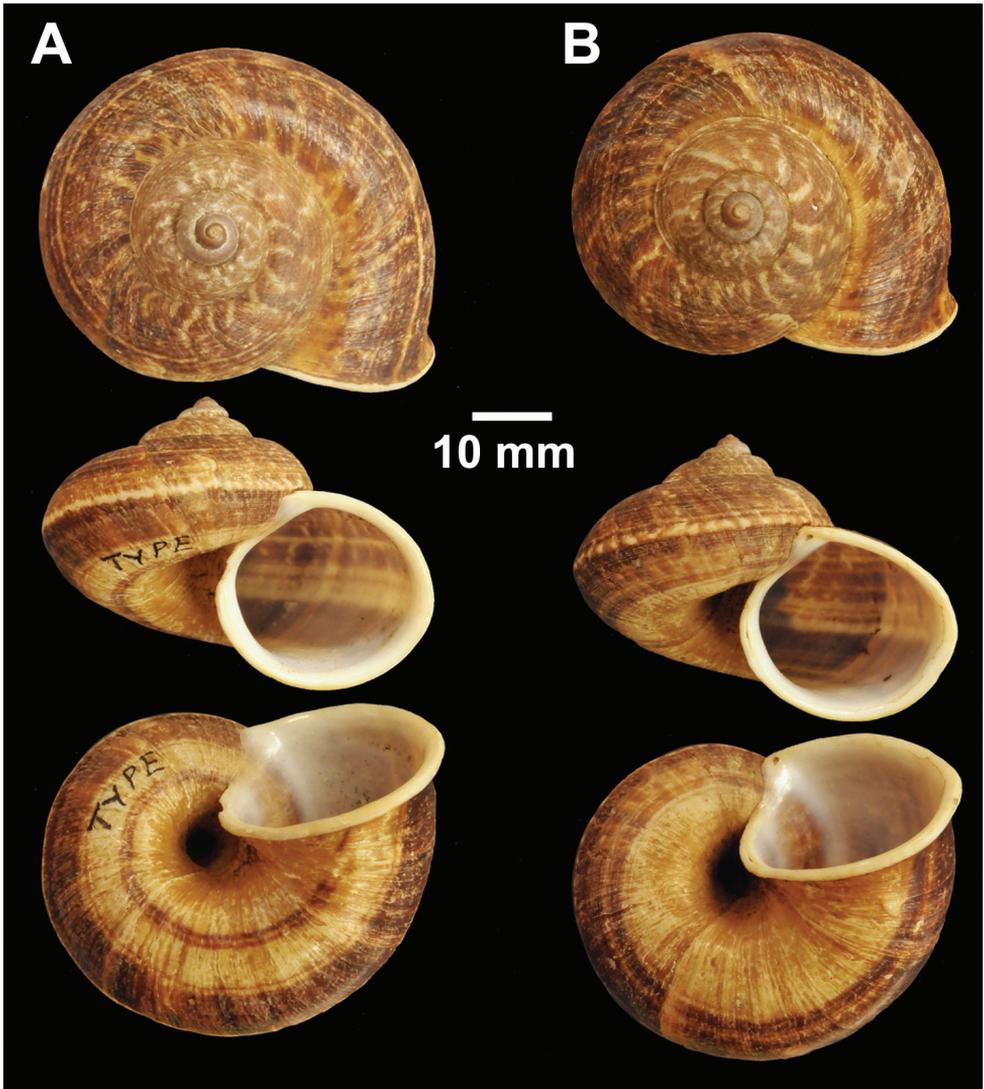


Figure 14. Types of *Cyclophorus* species. **A, B** *Cyclophorus muspratti* Godwin-Austen & Beddome, 1894 **A** holotype NHMUK 1903.7.1.1427/1, and **B** paratype NHMUK 1903.7.1.1427/2-4.

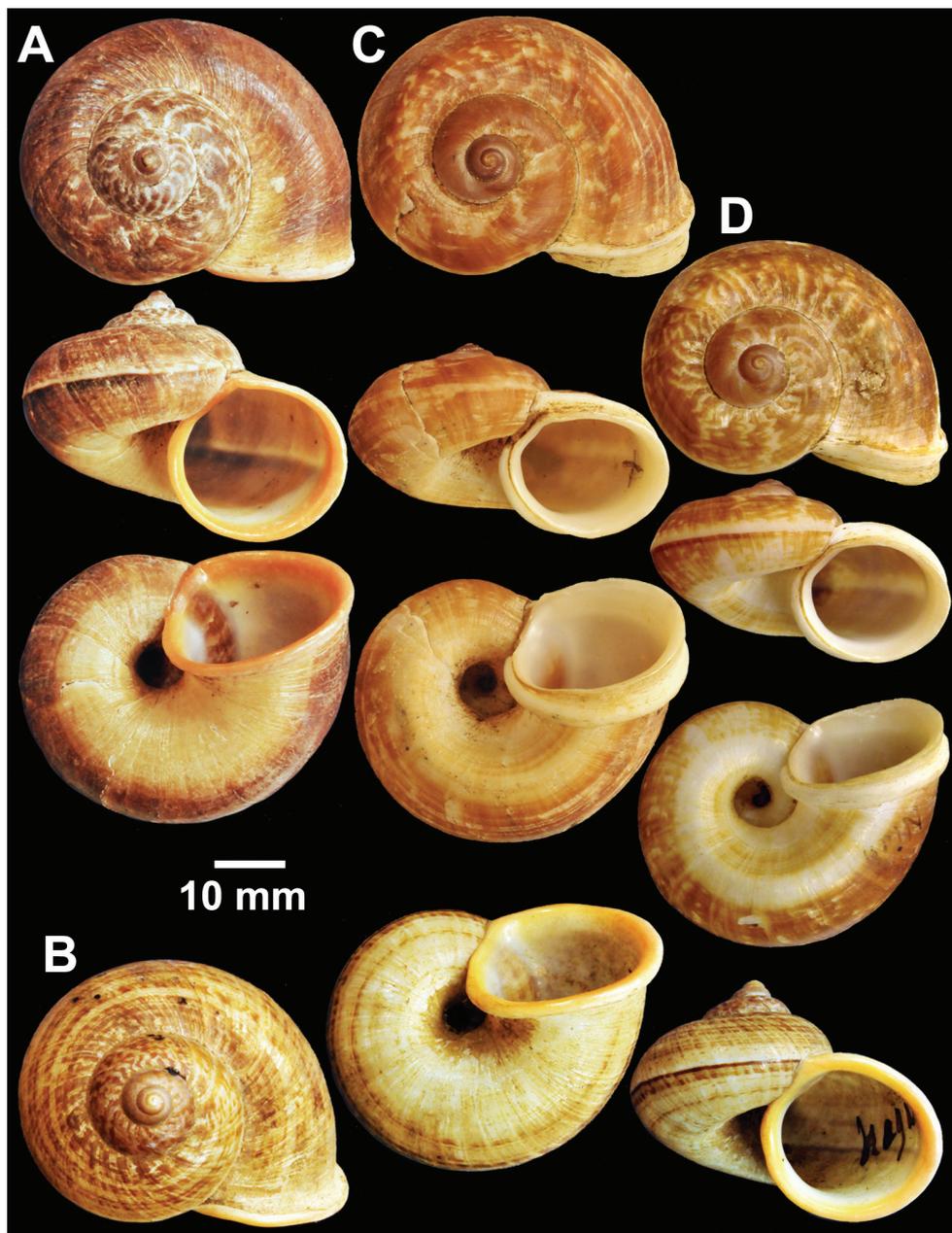


Figure 15. Types of *Cyclophorus* species. **A, B** *Cyclophorus nagaensis* Godwin-Austen & Beddome, 1894 **A** lectotype NHMUK 1903.7.1.1456/1, and **B** paralectotype NHMUK 1903.7.1.1456/2-4 **C, D** *Cyclophorus niabensis* Godwin-Austen, 1889 **C** lectotype NHMUK 1889.12.7.3, and **D** paralectotype NHMUK 1889.12.7.4.

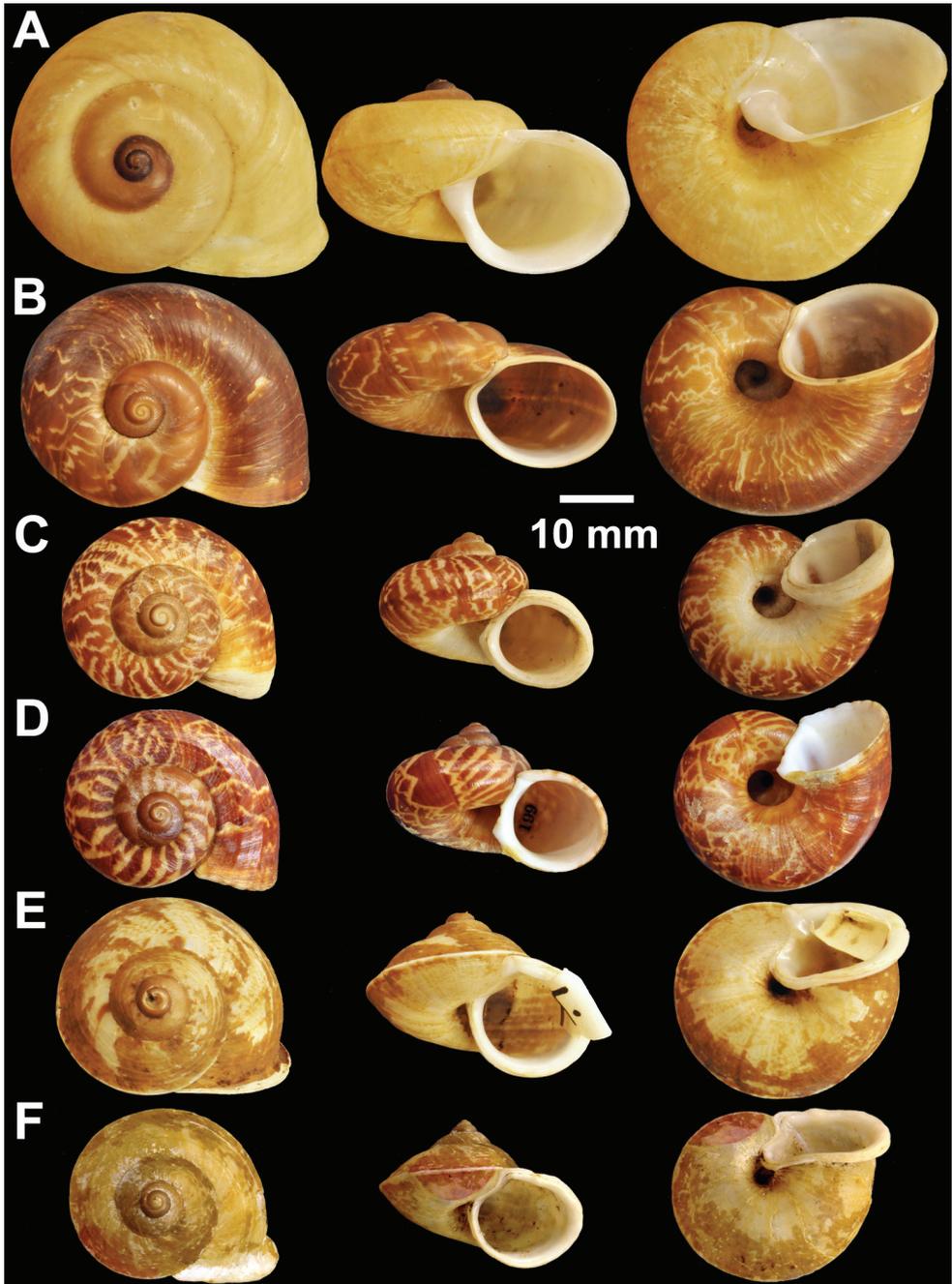


Figure 16. Types of *Cyclophorus* subspecies. **A** *Cyclophorus cochranei ochraceus* Godwin-Austen, 1889, lectotype NHMUK 1889.12.7.6. Types of *Cyclophorus* species **B** *Cyclophorus phlegethon* Godwin-Austen, 1889, holotype NHMUK 1998011 **C, D** *Cyclophorus picturatus* (Pfeiffer, 1854) **C** lectotype NHMUK 20130082/1, and **D** paralectotype NHMUK 20130082/2-3 **E, F** *Cyclophorus poeciloneurus* Godwin-Austen & Beddome, 1894 **E** lectotype NHMUK 1903.7.1.1522/1, and **F** paralectotype NHMUK 1903.7.1.1522/2.

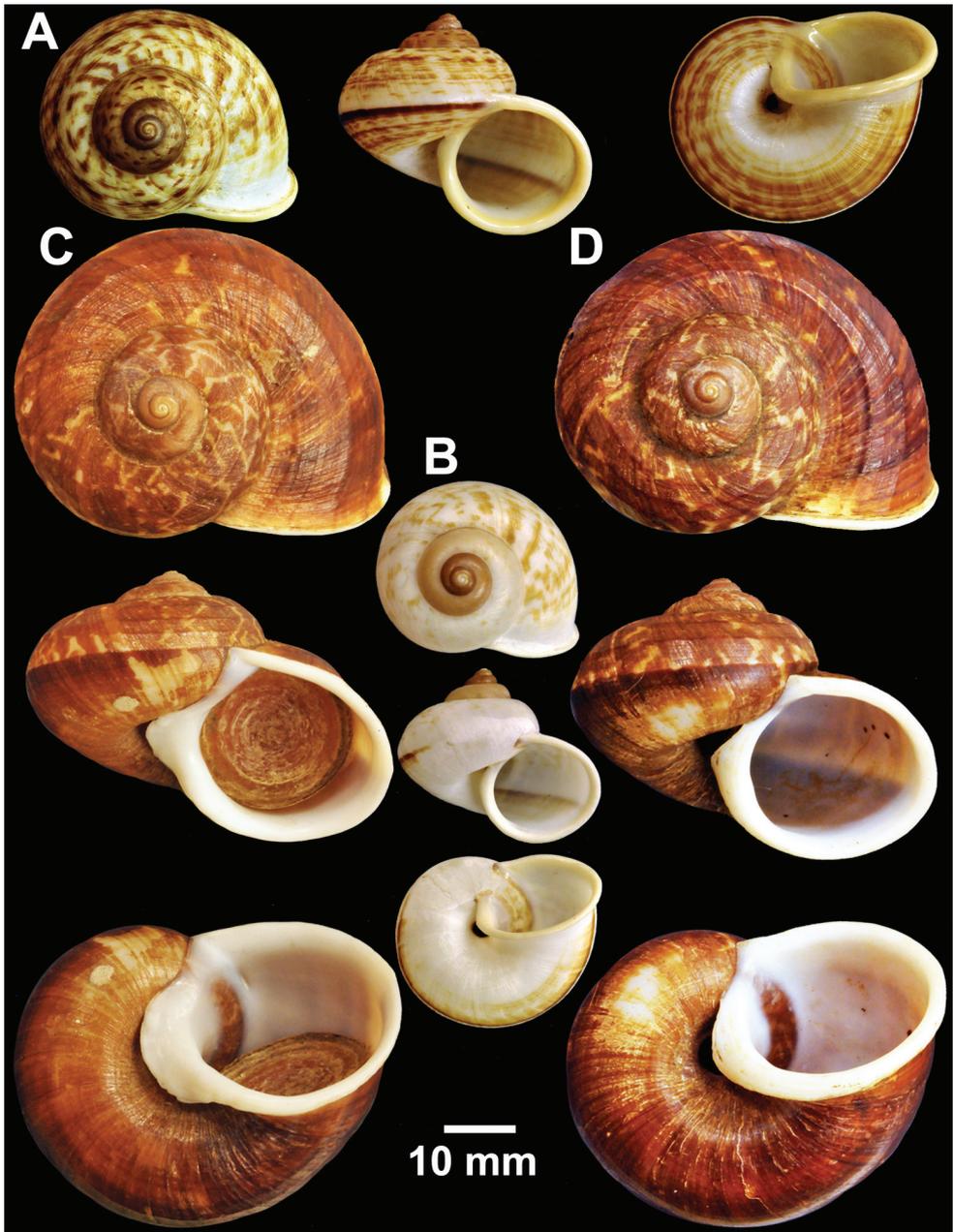


Figure 17. Types of *Cyclophorus* species. **A, B** *Cyclophorus fulguratus rangunensis* Kobelt, 1908 **A** lectotype NHMUK 20130091/1, and **B** paralectotype NHMUK 20130091/2-3 **C, D** *Cyclophorus eximus rouyeri* Bullen, 1906 **C** lectotype NHMUK 1906.1.16.51, and **D** paralectotype NHMUK 20130078.

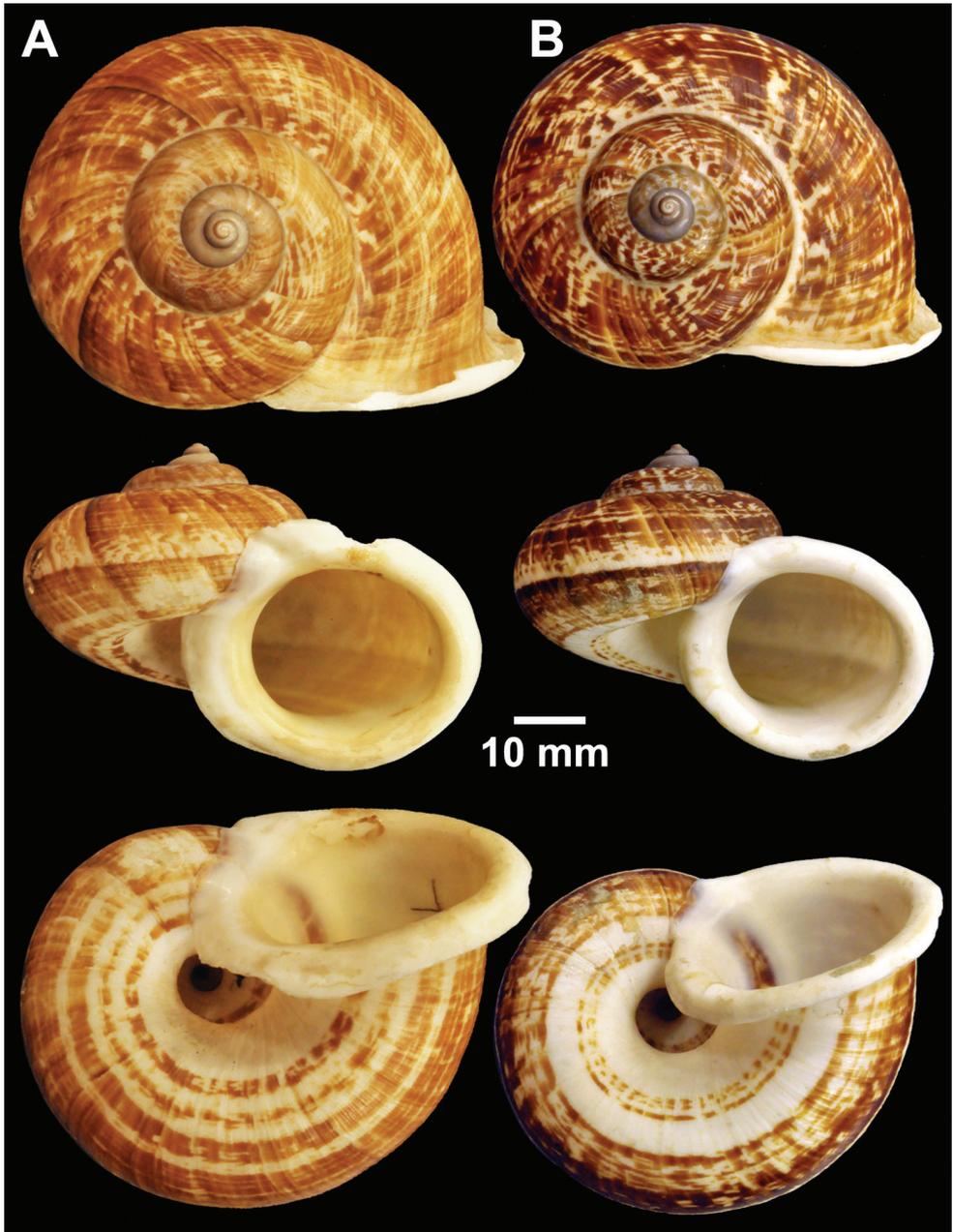


Figure 18. Types of *Cyclophorus* species. **A, B** *Cyclophorus saturnus* Pfeiffer, 1862 **A** lectotype NHMUK 20130119/1, and **B** paralectotype NHMUK 20130119/2-3.



Figure 19. Types of *Cyclophorus* species. **A** *Cyclophorus schepmani* Laidlaw, 1957, paratype NHMUK 1957.11.18.7 **B** *Cyclophorus serratizona* Hanley and Theobald, 1876, possible syntypes NHMUK 88.12.4.1955.

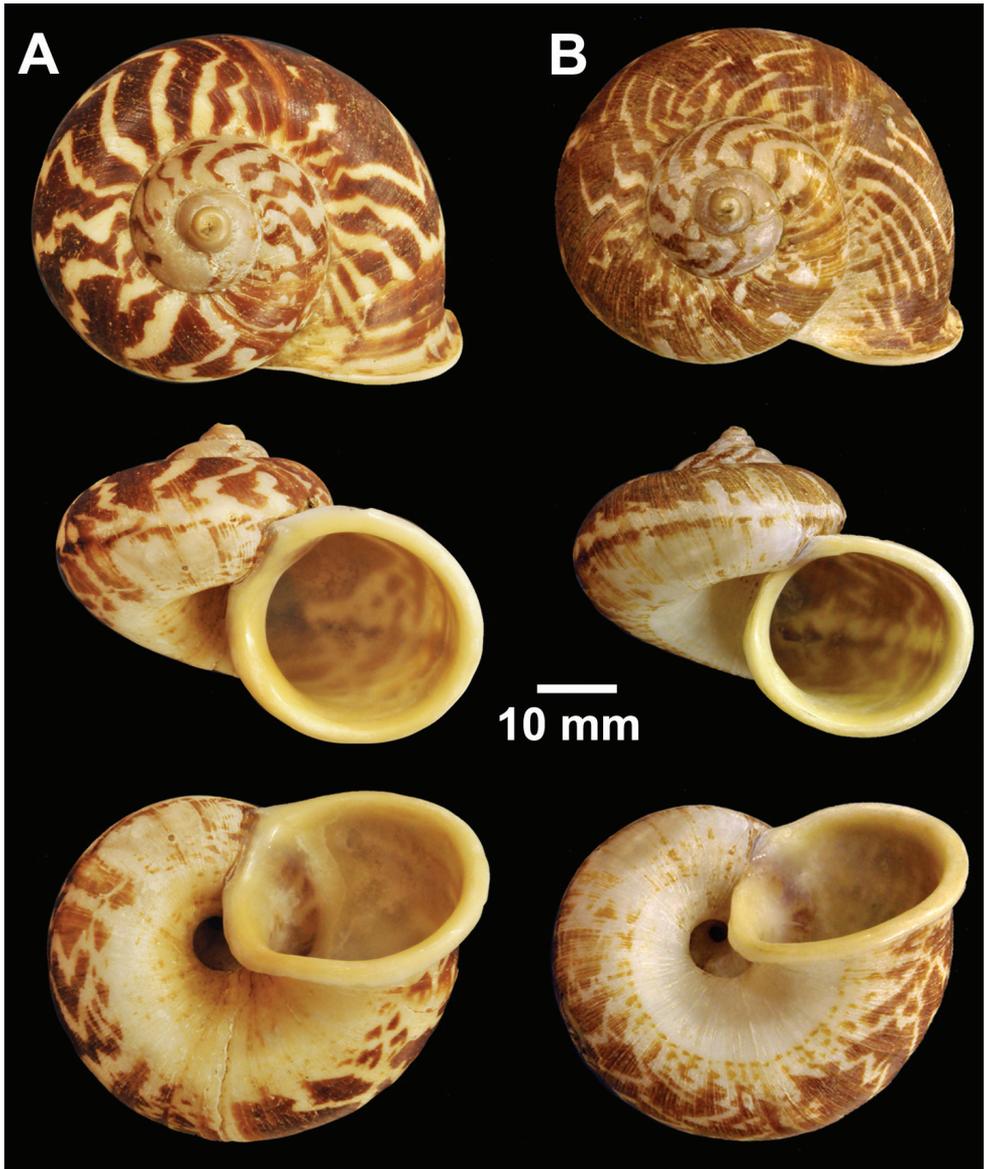


Figure 20. Types of *Cyclophorus* species. **A, B** *Cyclophorus siamensis* (Sowerby I, 1850) **A** lectotype NHMUK 20130088/1, and **B** paralectotype NHMUK 20130088/2.

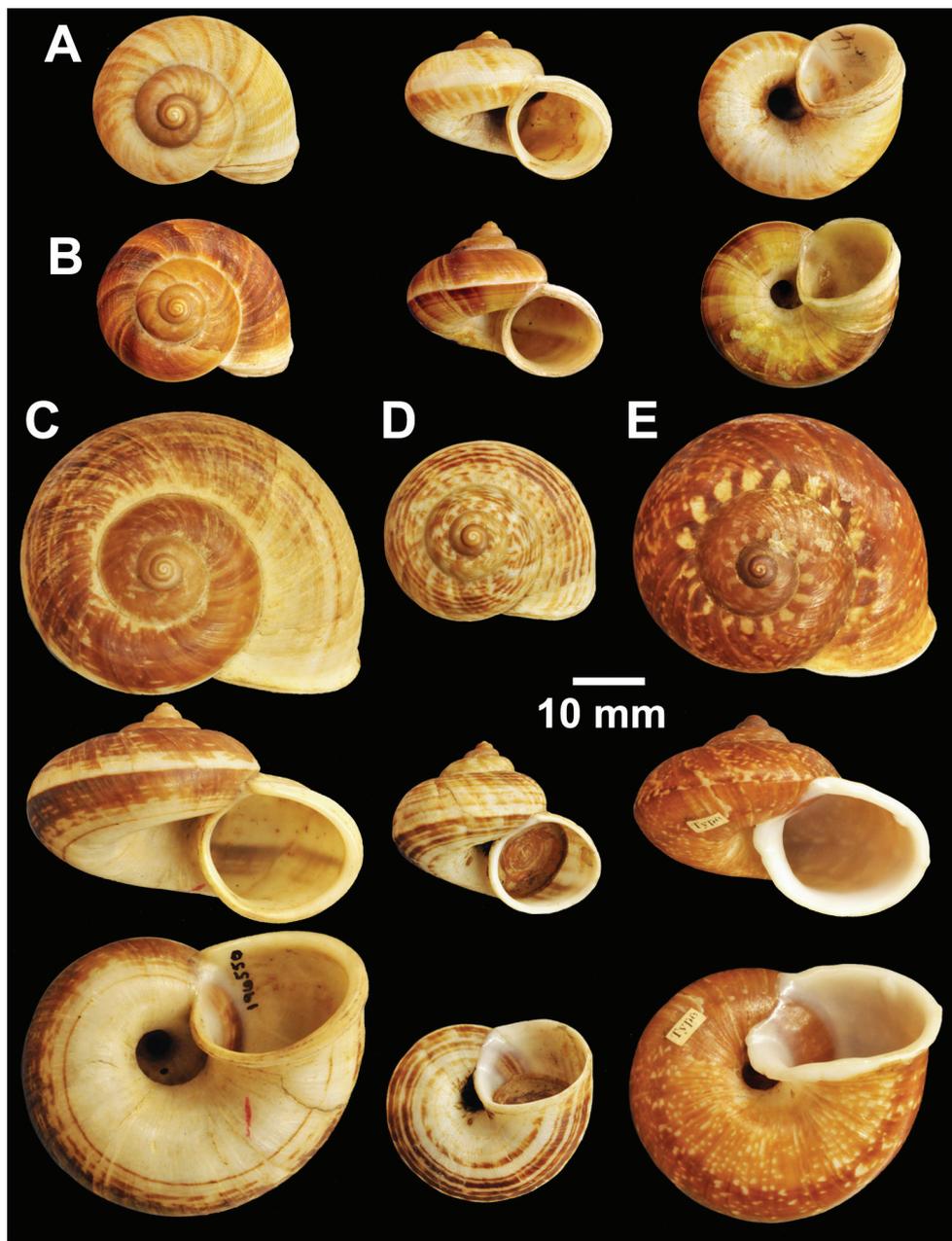


Figure 21. Types of *Cyclophorus* species. **A, B** *Cyclophorus spironema* (Pfeiffer, 1855) **A** lectotypes NHMUK 20130083/1, and **B** paralectotype NHMUK 20130083/2-3 **C** *Cyclophorus subblaevigatus* Blanford, 1869, lectotype NHMUK 196550 **D** *Cyclophorus taeniatus* (Pfeiffer, 1855), lectotype NHMUK 20130120 **E** *Cyclophorus talboti* Godwin-Austen, 1889, lectotype NHMUK 1889.12.7.7.

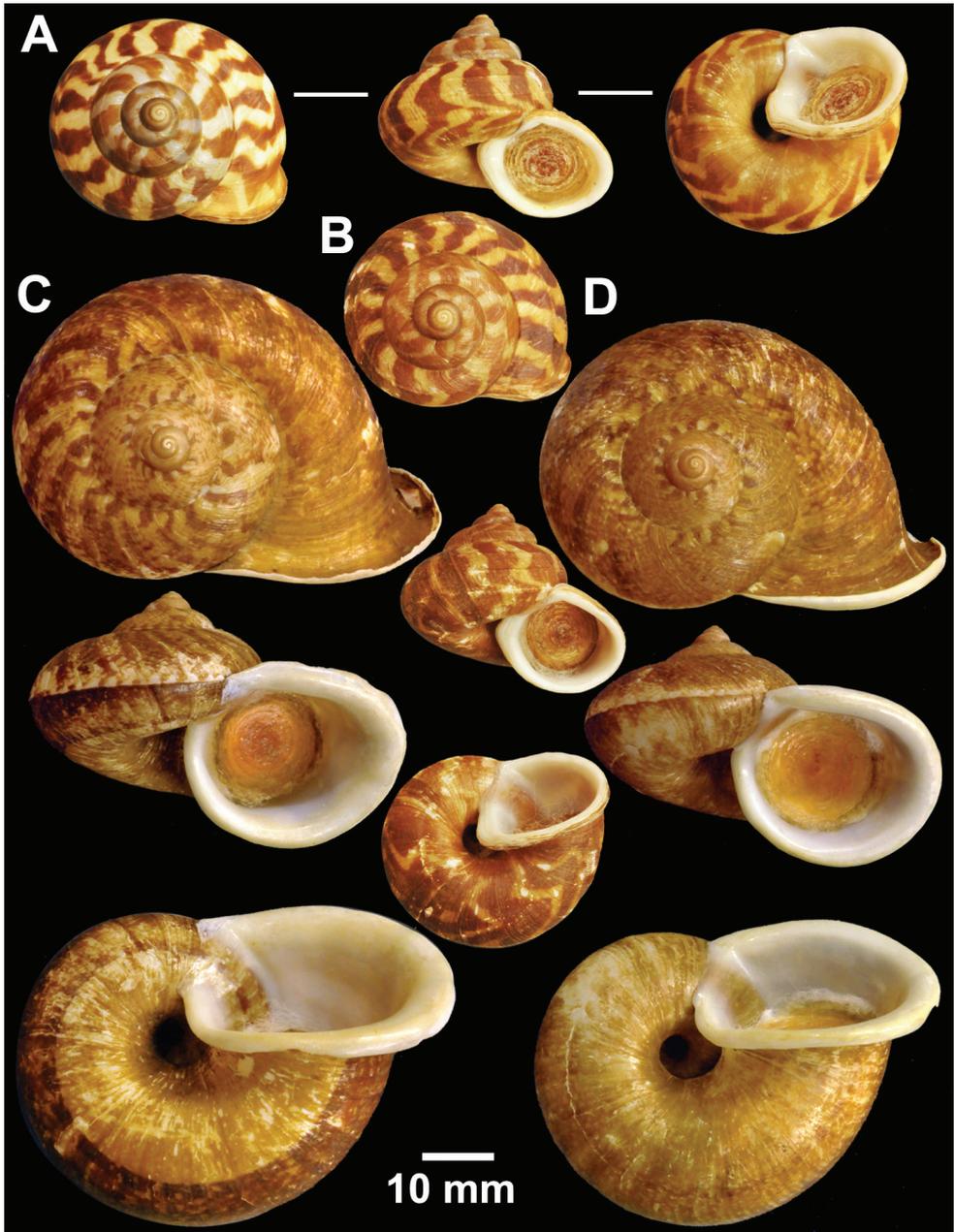


Figure 22. Types of *Cyclophorus* species. **A, B** *Cyclophorus tigrinus* (Sowerby I, 1843) **A** lectotype NHMUK 20110231/1, and **B** paralectotype NHMUK 20110231/2-3 **C, D** *Cyclophorus tuba* (Sowerby I, 1842) **C** lectotype NHMUK 20120064/1, and **D** paralectotype NHMUK 20120064/2.

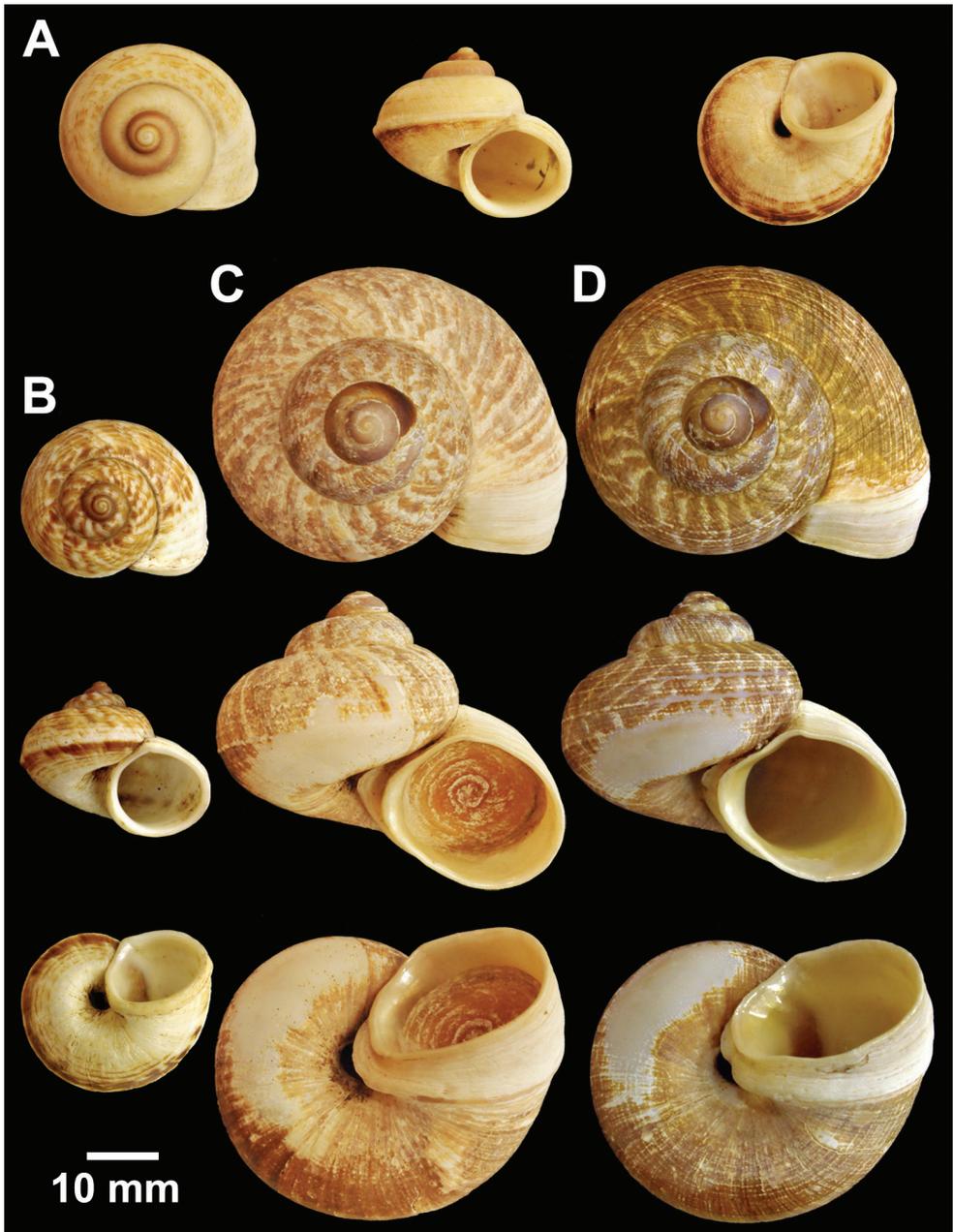


Figure 23. Types of *Cyclophorus* species. **A, B** *Cyclophorus turgidus* (Pfeiffer, 1851) **A** lectotype NHMUK 20040591/1, and **B** paralectotype NHMUK 20040591/2-3 **C, D** *Cyclophorus validus* (Sowerby I, 1842) **C** lectotype NHMUK 20110280/1, and **D** paralectotype NHMUK NHMUK 20110280/2-3.

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A new *Pseudophoxinus* (Teleostei, Cyprinidae) species from Asi River Drainage (Turkey)

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Abstract

Pseudophoxinus turani sp. n. is described from the İncesu Spring (Hassa-Hatay) drainage of Asi River, Turkey. It is distinguished from other Eastern Mediterranean Region *Pseudophoxinus* species by a combination of characters: lateral line incomplete, with 12–25 (commonly 16–21) perforated scales and 38–46+2–3 scales in lateral series (commonly 41–44 +2–3); 10–11 scale rows between the lateral line and dorsal-fin origin; 3–4 scale rows between the lateral line and the pelvic-fin origin; dorsal fin with 7½ branched rays; anal fin commonly with 7½ branched rays; 8–11 gill rakers on the first branchial arch; dorsal profile markedly convex with marked hump at the nape, ventral profile less convex than dorsal profile; a small, irregular, black blotch on the base of the caudal fin; mouth terminal, with slightly distinct chin, its corner not reaching vertical through anterior margin of eye; snout somewhat long, with rounded tip; and its length greater than eye diameter.

Keywords

Anatolia, Asi River, freshwater fishes, Leuciscinae, taxonomy

Introduction

Members of the cyprinid genus *Pseudophoxinus* are small minnows mostly found in cold springs, slow-flowing waters and clean lakes (Küçük et al. 2013). Speciation and phylogenetic relationships within the genus in Anatolia were first studied by Hrbek et al. (2004),

who argued that the Tohma Stream population (Fırat River drainage) (originally published as *Pseudophoxinus* new species, now *P. firati*) and *P. kervillei* from the Asi River form a separate lineage distinct from all other congeners in Central Anatolia, the Lakes Region and Büyük Menderes basins. A more comprehensive and detailed study based on mitochondrial and nuclear DNA data corroborates the hypothesis that the genus *Pseudophoxinus* is represented in Anatolia by two monophyletic lineages (Central Anatolian and Eastern Mediterranean Region clades) and noted uncertainty in Anatolian *Pseudophoxinus* species boundaries (Perea et al. 2010).

The original description of the Eastern Mediterranean Region species *P. kervillei* by Pellegrin (1911:109–110, 1928:120–121) includes the following information: lateral line incomplete, 37–42 scales in lateral series, 9–10 scale rows between lateral line and dorsal-fin origin, 7–8 scale rows between lateral line and the pelvic-fin origin, D 11, A 10, P 13, V 8. The distribution area originally given as Asi River, Adana and Islahiye near Osmaniye (Pellegrin 1928:121), is restricted to Jordan, Litani and Asi rivers basins according to Krupp (1985), who described a *Phoxinellus* (= *Pseudophoxinus*) sp. from Hupnik Stream (near Islahiye, 22 km southeast Gaziantep), a drainage of Asi River, with a shorter lateral line (0–18 scales vs. 4–27 in *P. kervillei*), more gill rakers and more branched anal-fin rays. Since then this population hasn't been studied and couldn't be relocated at site during our surveys in June 2012 and October 2013. Bogutskaya (1997:177–178) wrote that the *Pseudophoxinus* specimens from the Ceyhan River (ZMH 1103: Hamburg Zoological Museum, now *P. zekayi*) and İncesu Spring (ZMH 8001) (mentioned in the original text as Seyhan tributary, although it is a tributary of Asi) differed from Asi River *P. kervillei* in having more scales in the lateral series (55–60 vs. 35–50 in *P. kervillei*) and presence of 25–34 perforate scales (4–17 in *P. kervillei*). Perea et al. (2010) also tentatively identified the *Pseudophoxinus* population from İncesu Spring (Hassa, Hatay) as *P. cf. kervillei* due to molecular distinction of the population from *P. kervillei* (Asi River).

Our evaluation of morphological features and the distribution areas of Eastern Mediterranean Region species *P. firati*, *P. kervillei*, *P. zeregi* and *P. zekayi* indicates that the İncesu (Hassa, Hatay) specimens represent a new species distinct from the Asi River basin *P. kervillei*, which is described below.

Materials and methods

Fish specimens were collected by pulsed DC electrofishing equipment, killed by over anaesthetization and fixed in 5% formalin. Material is deposited in: IFC-ESUF, Inland Fishes Collection, Eğirdir Fisheries Faculty of Süleyman Demirel University. Counts and measurements follow Kottelat and Freyhof (2007). All measurements were point to point and made with digital calipers (0.01 mm sensitive). Other metrics include head width₁ (the distance between the anterior eye margins), head width₂ (the distance between the posterior eye margins), head width₃ (head width at the nape), head depth₁ (head depth through the eye), head depth₂ (head depth at the nape), and the snout width (measured at level of the nostrils). The perforated lateral-line scales were counted from the anteriormost scale (the first one

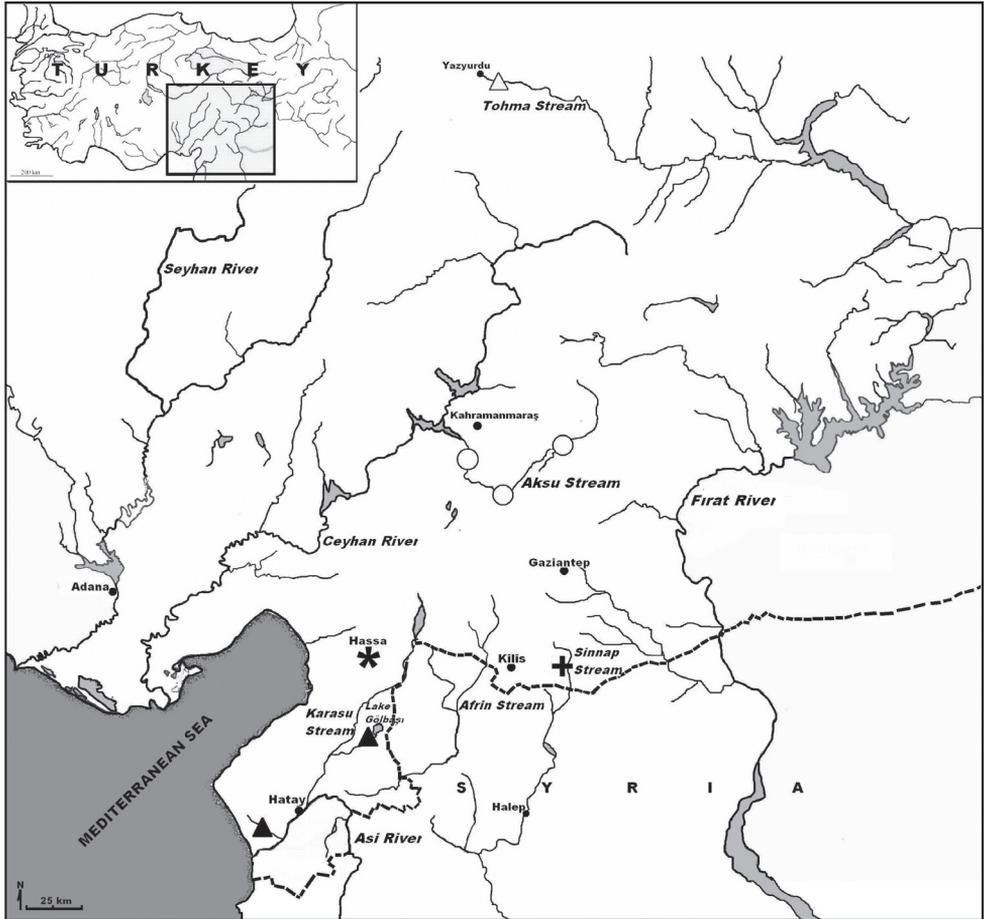


Figure 1. Map showing localities of Eastern Mediterranean Region *Pseudophoxinus* species group (Δ *P. firati*, \blacktriangle *P. kervillei*, \ast *P. turani* sp. n., \circ *P. zekayi*, $+$ *P. zeregi*).

to touch the shoulder girdle) to the posteriormost one; scales in lateral series were counted along the midlateral line from the first one to touch the shoulder girdle to the last scale at the end of the hypural complex; scales on the caudal fin itself are indicated by “+”; the last two branched dorsal and anal fin rays articulating on a single pterygiophore were counted as 1½. The vertebral counts were obtained from radiographs and counted following Naseka (1996); abdominal vertebrae were counted from the first Weberian vertebra to the one just anterior to the first caudal vertebra (the most anterior vertebra that has a fully developed haemal spine; the last complex vertebra bearing hypurals was included in the count of total and caudal vertebrae. Cephalic sensory canals were studied under a stereomicroscope.

The morphometric characters of the two species of *Pseudophoxinus* from Turkey were compared by Principal Component Analysis (PCA) using a covariance matrix on log-transformed measurements and counts with the software package PAST version 1.8 (Hammer et al. 2001).

Results

Pseudophoxinus turani sp. n.

<http://zoobank.org/98DF0D2B-6917-44DA-8EAC-E524C0BEB787>

http://species-id.net/wiki/Pseudophoxinus_turani

Figures 2, 3

Holotype. IFC-ESUF 03-1002, 71.3 mm SL; Turkey, Hatay Prov., Hassa Country, İncesu Spring, Asi River drainage, 36°47.36'N, 36°30.48'E, 20 October 2013, coll. F. Küçük and A. Küçük.

Paratypes. IFC-ESUF 03-1003, 20, 52.1–93.4 mm SL, same as holotype.

Diagnosis. *Pseudophoxinus turani* is distinguished from all other species of Eastern Mediterranean Region *Pseudophoxinus* (*P. firati*, *P. kervillei*, *P. zeregi*, *P. zekayi*) by the following unique combination of characters: head short, its length 26–28% SL, approximately equal to or slightly shorter than body depth; mouth terminal, with slightly distinct chin, its corner not reaching vertical through anterior margin of eye; eye small, its diameter 25–29% HL, smaller than snout length; lateral line incomplete, with 12–25 (commonly 16–21) perforated scales and 38–46+2–3 scales in lateral series (commonly 41–44 +2–3); 10–11 scale rows between lateral line and dorsal-fin origin; 3–4 scale rows between lateral line and the pelvic-fin origin; 8–11 (rarely 13) gill rakers on the first branchial arch; pharyngeal teeth 5–4, slightly serrated and hooked at tip.

Description (See Figs 2, 3 for general appearance and Tables 1, 2 for morphometric and meristic data). Body deep, its depth at dorsal-fin origin 26–29% SL, mean 27.8, and laterally compressed. Dorsal profile markedly convex with marked hump at nape, ventral profile less convex than dorsal profile. Dorsal-fin origin situated behind base of pelvic-fin. Predorsal length 56–60% SL, mean 58.2 and prepelvic length 51–54% SL, mean 52.4. Head short, its length 26–28% SL, mean 26.9, approximately equal to or slightly shorter than body depth, upper profile straight or slightly convex on interorbital area and markedly convex on snout. Mouth terminal, with slightly marked chin, its corner not reaching vertical through anterior margin of eye. Eye small, its diameter 25–29% HL, mean 26.6. Snout somewhat long, with rounded tip, its length 27–31% HL,



Figure 2. *P. turani* sp. n. holotype, IFC-ESUF 03-1002, 71.3 mm SL, Turkey: Hatay prov.: Hassa, İncesu Spring, Asi River drainage.



Figure 3. *P. turani* sp. n. paratype, IFC-ESUF 03-1003, 66.0 mm SL, Turkey: Hatay prov.: Hassa, İncesu Spring, Asi River drainage.

Table 1. Morphometry of *P. turani* sp. n. (holotype IFC-ESUF 03-1002, paratypes IFC-ESUF 03-1003, n=20) and *P. kervillei* (IFC-ESUF 03-0987, n=21).

	<i>P. turani</i>		<i>P. kervillei</i>
	Holotype	Paratypes	
In percent of standard length			
Head Length	26.8	26.0-27.5 (26.9) ±0.001	24.8-29.9 (27.5) ±0.003
Body depth of dorsal- fin origin	26.0	25.9-29.2 (27.8) ±0.001	24.9-29.5 (27.8) ±0.003
Predorsal distance	57.8	55.9-59.6 (58.2) ±0.002	54.9-59.5 (56.9) ±0.003
Prepelvic distance	52.3	50.7-54.3 (52.4) ±0.002	50.9-54.7 (52.8) ±0.003
Preanal distance	73.5	70.8-76.2 (73.6) ±0.003	70.3-77.9 (72.8) ±0.006
Distance between pectoral and anal-fin origins	47.7	45.4-49.5 (48.1) ±0.003	43.7-49.7 (46.6) ±0.005
Distance between pectoral and pelvic-fin origins	25.5	24.1-26.7 (25.9) ±0.002	21.8-27.2 (23.9) ±0.004
Distance between pelvic and anal-fin origins	21.7	20.5-23.9 (22.1) ±0.002	20.7-23.9 (22.4) ±0.003
Dorsal fin depth	22.4	21.9-24.8 (23.5) ±0.001	19.6-25.3 (22.7) ±0.005
Dorsal fin length	12.4	11.7-13.9 (12.9) ±0.001	11.7-12.9 (12.5) ±0.003
Anal fin depth	16.9	16.8-19.3 (18.1) ±0.001	16.1-18.9 (17.8) ±0.002
Anal fin length	11.2	10.9-12.1 (11.3) ±0.004	10.1-13.6 (11.6) ±0.003
Pectoral fin length	20.1	16.2-20.8 (19.3) ±0.002	17.5-23.1 (19.0) ±0.004
Pelvic fin length	17.1	14.7-19.9 (17.8) ±0.003	16.3-18.2 (16.9) ±0.001
Caudal peduncle length	20.1	17.0-20.1 (18.4) ±0.002	15.2-20.3 (17.5) ±0.004
Caudal peduncle depth	12.5	11.7-13.9 (12.8) ±0.001	10.9-12.9 (12.1) ±0.002
In percent of head length			
Snout length	28.5	26.8-31.5 (30.4) ±0.003	25.7-31.4 (28.0) ±0.005
Eye diameter	25.7	24.8-29.3 (26.6) ±0.003	26.9-32.7 (29.5) ±0.005
Interorbital distance	36.7	36.2-40.9 (38.9) ±0.003	35.1-42.3 (38.4) ±0.006
Head width 1	36.4	32.6-38.8 (36.3) ±0.004	29.6-35.7 (32.7) ±0.005
Head width 2	47.4	47.4-52.4 (50.5) ±0.002	44.8-52.1 (48.4) ±0.006
Head width 3	53.5	51.6-58.1 (54.9) ±0.003	50.1-56.4 (53.2) ±0.006
Head depth 1	56.5	54.4-63.8 (57.1) ±0.005	53.1-56.3 (55.1) ±0.005
Head depth 2	77.6	74.5-82.8 (78.8) ±0.007	71.8-79.0 (74.2) ±0.006
Internostril distance	20.9	20.2-24.8 (22.2) ±0.003	19.2-25.4 (22.2) ±0.004
Mouth width	26.5	23.1-29.4 (27.1) ±0.003	23.3-27.7 (25.2) ±0.004
Lower jaw length	36.9	34.9-42.7 (38.6) ±0.004	35.0-41.2 (38.2) ±0.004

Table 2. Meristic features of the Eastern Mediterranean Region *Pseudophoxinus* species group (from comparative material).

Species	Lateral series scales	Lateral line scales	Pharyngeal teeth	Gill rakers	Vertebral formula
<i>P. frati</i>	41–49+1–2	35–51	5–5 (4)	6–7	37–38:22+16–17
<i>P. kervillei</i>	37–44+2–3	4–17	5–4	7–8	35–36:19–20+16–17
<i>P. turani</i> sp. n.	38–46+2–3	12–25	5–4	8–11(13)	36–38:21–22+16–17
<i>P. zekayi</i>	40–46+1–2	36–43	5–5	7–9	37–39:21–22+15–17
<i>P. zeregi</i>	54–59+2–3	47–53	5–4	7–9	36–38:19–21+16–17

mean 30.4, greater than eye diameter. Caudal-peduncle length 17–20% SL, mean 18.4; caudal-peduncle length 1.3–1.7, mean 1.5, times its depth. Lateral line incomplete, commonly not reaching the level of anus, 12–25 perforated scales, 38–46+2–3 scales in lateral series. Dorsal fin with 3 simple and 7½ branched rays, outer margin straight or slightly convex. Anal fin with 3 simple and 6½ (2 specimens)–7½ (19 specimens) branched rays, outer margin straight or slightly convex. Pectoral fins with 11–12 (rarely 13) branched rays, outer margin convex. Pelvic fins with 6 branched rays, outer margin convex. Caudal fin forked, lobes rounded. No pelvic axillary lobe and keel between posterior pelvic fin base and anus. Pharyngeal teeth 5–4, slightly serrated, hooked at tip. Gill rakers short, with 8–11 (rarely 13) on outer side of first gill arch. Scales oval, with numerous radii posteriorly. Total vertebrae 36–38, 21–22 abdominal and 16–17 caudal vertebrae, vertebral formulae: 36–38:20–21+16–17.

Sexual dimorphism. There is no sexual dimorphism between males and females

Coloration. Ground color of formalin-preserved adults and juveniles dark grey on back and upper part of flank, yellowish on lower part of flank and belly. Dark grey stripe (its width 1 to 2 times eye diameter) on the middle of flank from posterior margin of operculum to caudal peduncle, distinct in both anterior and posterior parts of body. Caudal, dorsal and anal fins grey; pectoral and pelvic fins light grey. Black spots present on rays of all fins, additionally on the dorsal-fin base. A small black blotch of pigment present on caudal-fin base. Peritoneum grayish to blackish, with numerous crystal-shaped black spots.

Etymology. The species is named after Davut Turan (Recep Tayyip Erdoğan University, Rize), in appreciation for his contributions to our knowledge of the fish fauna of Anatolia.

Discussion

As stated by Küçük et al. (2013), unlike the central and western Anatolian species, which differ from one another in complex morphological features, the Eastern Mediterranean *Pseudophoxinus* species (mentioned as Levant species) are morphologically quite similar with the exception of *P. zekayi*, which differs from the others in having a complete lateral line.



Figure 4. *P. kervillei* IFC-ESUF 03-0987, 73.2 mm SL, Turkey: Hatay prov.: Lake Gölbaşı, Asi River drainage.

Below we compare *P. turani* from the İncesu Spring, a drainage of Asi River, with the Eastern Mediterranean region *Pseudophoxinus* species group: *P. kervillei* from Gölbaşı Lake (Asi River drainage), *P. zekayi* from Aksu Stream (Ceyhan River drainage), *P. zeregi* from Sinnap Stream (Kuveik River drainage), and *P. firati* from Tohma Stream (Fırat River drainage) (Pellegrin 1911; 1928; Bogutskaya 1997; Bogutskaya et al. 2007). *Pseudophoxinus turani* is easily distinguished from *P. kervillei* by its terminal mouth (vs. slightly superior) and rounded snout (vs. slightly rounded). It is further distinguished from *P. kervillei* by having more gill rakers on the outer side of the first gill arch (8–11, rarely 13, vs. 7–8), usually more lateral-line scales (12–25, vs. 4–17), more abdominal vertebrae (21–22, vs. 19–20), usually more total vertebrae (36–38, vs. 35–36) and sometimes fewer branched pelvic-fin rays (6 vs. 6–7). Besides the differences listed above *P. turani* has a smaller eye diameter and longer snout than *P. kervillei*.

Pseudophoxinus turani and *P. kervillei* were also compared by Principal Component Analysis (PCA) using 27 morphometric characters. The PCA clearly separated *Pseudophoxinus turani* from *P. kervillei* (Fig. 5). Variables loading on the first metric PC I–II are given in Table 3.

Pseudophoxinus turani is distinguished from *P. zeregi* by having fewer lateral-line scales (12–25, vs. 47–53), fewer lateral series scales (38–46+2–3, vs. 54–59+2–3), fewer scales between lateral line and dorsal-fin origin (10–11, vs. 11–13) and usually more gill rakers on first gill arch (8–11, rarely 13, vs. 7–9). In *Pseudophoxinus turani*, membranes of fins are grey and rays have black spots, while in *P. zeregi* membrane of fins are hyaline and rays lack black spots.

Pseudophoxinus turani is clearly separable from *P. zekayi* by having an incomplete lateral line (vs. complete), fewer lateral-line scales (12–25 vs. 36–44), fewer pharyngeal teeth (5–4, vs. 5–5) and a longer snout (28.5–31.7 % HL, mean 30.3, vs. mean 26.01 % HL). In *P. turani*, eye diameter is smaller than snout length while in *P. zekayi*, eye diameter is equal to or greater than snout length.

Pseudophoxinus turani is distinguished from *P. firati* by having fewer lateral-line scales (12–25 vs. 35–51) and more gill rakers on the outer side of the first gill arch

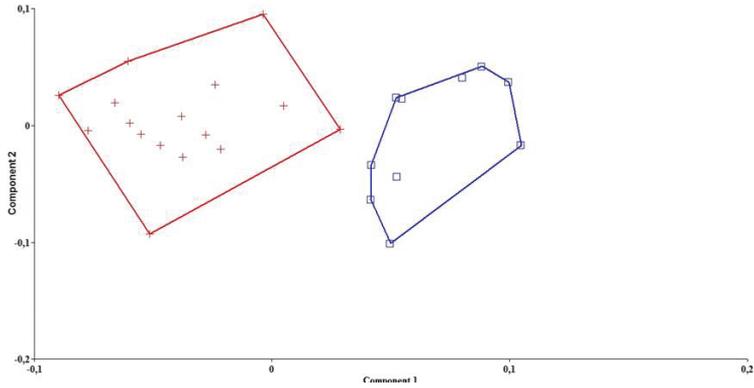


Figure 5. A scatter plot of the scores of the first two principal components (PC I, PC II) for 28 specimens of two *Pseudophoxinus* species, *P. turani* sp. n. (+) and *P. kervillei* (□), based on 27 morphometric characters.

Table 3. Character loading on principal components I–II for 27 measurements taken on 28 specimens of two *Pseudophoxinus* species (*P. turani* sp. n. and *P. kervillei*).

Morphometric features		
In percent of standard length	PC I	PCA II
Head Length	0.052	-0.162
Body depth of dorsal- fin origin	-0.030	-0.144
Predorsal distance	-0.104	-0.043
Prepelvic distance	0.006	-0.048
Preanal distance	-0.055	-0.096
Distance between pectoral and anal-fin origins	-0.128	-0.143
Distance between pectoral and pelvic-fin origins	-0.296	-0.084
Distance between pelvic and anal-fin origins	0.011	-0.259
Dorsal fin depth	-0.161	-0.101
Dorsal fin length	-0.099	0.021
Anal fin depth	-0.060	0.074
Anal fin length	0.274	0.166
Pectoral fin length	-0.106	-0.306
Pelvic fin length	-0.231	0.095
Caudal peduncle length	-0.243	0.132
Caudal peduncle depth	-0.275	-0.208
In percent of head length		
Snout length	-0.327	0.138
Eye diameter	0.363	0.261
Interorbital distance	-0.022	0.209
Head width 1	-0.426	0.077
Head width 2	-0.130	0.124
Head width 3	-0.128	0.076
Head depth 1	-0.172	0.129
Head depth 2	-0.249	0.181
Internostril distance	0.027	0.356
Mouth width	-0.136	0.491
Lower jaw length	0.006	0.253

(8–11, rarely 13, vs. 6–7). *P. turani* is also distinguished from *P. firati* by having a black spot on base of caudal fin (vs. lacking), slightly shorter head length (26.0–27.5, mean 26.9 %SL, vs. mean 28.6), 3 simple dorsal-fin rays (vs. commonly 4), and more scales between lateral-line and dorsal-fin origins (10–11, vs. commonly 9).

Our data on meristic features of the Eastern Mediterranean *Pseudophoxinus* (Table 2) are largely compatible with previously published counts: Heckel (1843) counted 57–66 perforated scales on the lateral line of the type species, *P. zeregi*, from the Kuveik River near Aleppo, whereas we counted 47–53 scales in our material from Sinnap Stream (Kuveik River drainage) (We believe that Heckle (1843) were counted scales in lateral series along the midlateral line). Lateral series and lateral line scale counts of *P. kervillei* are compatible with that of Pellegrin (1928) and Küçük et al. (2013). Meristic data of *P. firati* and *P. zekayi* are also found largely to be in conformity with Bogutskaya et al. (2007) and Küçük et al. (2013).

Comparative material (all from Turkey)

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- P. kervillei*: IFC-ESUF 03-0987, 26, 60.7–84.9 mm SL, Hatay prov.: Lake Gölbaşı-Kırıkhan, F.Küçük, D.Turan, S.S. Güçlü, 01 July 2012; 03-0988, 25, 27.4–56.0 mm SL, Hatay prov.: Meydan Village-Samandağ, F.Küçük, D.Turan, S.S. Güçlü, H.Temizkan, 30 June 2012.
- P. zekayi*: IFC-ESUF 03-1007, 32, 28.5–62.1 mm SL, Kahramanmaraş prov.: Aksu Stream, F.Küçük, D.Turan, S.S. Güçlü, 29 June 2012.
- P. zeregi*: IFC-ESUF 03-1011, 47, 33.9–64.5 mm SL, Kilis prov.: Sinnap Stream, F.Küçük, D.Turan, S.S. Güçlü, M. Kamer, C. Kaya, 04 November 2012 and 26 June 2013; IFC-ESUF 03-1012, 4, 36.3–64.5 mm SL, Kilis prov.: Sinnap Stream, İnanlı Village, C. Kaya, E. Gürlek, 26 June 2013.

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The ant genus *Tetramorium* Mayr in the Afrotropical region (Hymenoptera, Formicidae, Myrmicinae): synonymisation of *Decamorium* Forel under *Tetramorium*, and taxonomic revision of the *T. decem* species group

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Abstract

In this study we synonymise the genus *Decamorium* Forel under *Tetramorium* Mayr, revise the new *T. decem* species group by providing a diagnosis of the group, an illustrated identification key to species level, and worker-based species descriptions for all five species, which include diagnoses, discussions, images, and distribution maps. The following species are revised in this study: *T. decem* Forel, **comb. r.**, *T. raptor* **sp. n.**, *T. uelense* Santschi, **comb. r.**, *T. ultor* Forel, **comb. r.**, **stat. r. & stat. n.**, and *T. venator* **sp. n.** In addition, we also designate lectotypes for *T. decem*, *T. uelense*, and *T. ultor*.

Keywords

Afrotropical region, *Decamorium*, taxonomy, Tetramoriini, *Tetramorium*, *T. decem* species

Introduction

The genus *Tetramorium* Mayr is globally distributed and with 520 valid species it represents one of the most species-rich ant genera (Bolton 2014). The vast majority of these are found in the tropics of the Old World. In the Afrotropical and Malagasy regions, *Tetramorium* is hyperdiverse by the definitions of Wilson (2003) and Moreau (2008). In Madagascar and the neighbouring islands of the Indian Ocean, recent studies have revealed a highly endemic and astonishingly diverse *Tetramorium* fauna consisting of around 120 species (Bolton 1979; Hita Garcia and Fisher 2011, 2012a, 2012b, unpublished). The known Afrotropical *Tetramorium* fauna was thoroughly revised by Bolton (1976, 1980, 1985), parts of which were recently updated by Hita Garcia et al. (2010) and Hita Garcia and Fisher (2011, 2013), producing a current total of 224 species. In addition, there are at least 100 more undescribed Afrotropical species located in several museum collections awaiting formal description (FHG, unpublished data). Traditionally, what is now considered as *Tetramorium* was divided into the genera *Atopula* Emery, *Macromischoides* Wheeler, *Tetramorium*, and *Xiphomyrmex* Forel until Bolton's genus-level revision (1976). The name *Tetramorium* was used for a much smaller subset of species with twelve antennal segments. Bolton provided ample evidence for the artificiality of these genera and synonymised them under *Tetramorium*. Particularly noteworthy is the fact that the previous separation of *Xiphomyrmex* (11-segmented antennae) from *Tetramorium* (12-segmented antennae) was based solely on the difference in the antennomere count; Bolton showed this character to be variable in other tetramoriine genera.

Forel (1913a) described *Decamorium* Forel as a subgenus of *Tetramorium* on the basis of the ten-segmented antennae and the very pronounced and deep antennal scrobes. A few years later Arnold (1917) followed Forel and also treated *Decamorium* as a subgenus of *Tetramorium*. He based his decision on the ten-segmented antennae, the well-defined and deep antennal scrobes, the obsolete lateral ridges of the clypeus, and the strongly swollen tibiae and femorae in the worker caste. Nevertheless, apart from these two works (Forel 1913a; Arnold 1917), most other authors (and later even Forel himself) have treated *Decamorium* as a genus distinct from *Tetramorium* (Emery 1914, 1924; Forel 1917; Wheeler 1922; Bernard 1953; Bolton 1973, 1976, 1995). In his classification of the Myrmicinae, Emery (1914) was the first to treat *Decamorium* as a "genus" rather than a subgenus, although he did not provide any explanation of his decision. Later, in his "Genera Insectorum", Emery (1924) continued to list *Decamorium* as a genus. In that work he re-described the genus and separated it from the other then known tetramoriine genera, again on the basis of the ten-segmented antennae of the workers and queens. All subsequent authors listed *Decamorium* as a genus without taxonomic treatment until Bolton's (1976) revision of the tribe Tetramoriini. As mentioned above, he diagnosed most of the currently valid genera of the tribe and also reviewed *Decamorium*. Bolton (1976) clearly stated that the separation of *Decamorium* from *Tetramorium* on the grounds of the reduced antennal count, reduced clypeal shield, and differences in mandibular dentition was relatively dubious. He doubted

that these characters would persist to diagnose *Decamorium* in the future. However, since then nothing more on the generic limits or alpha taxonomy of *Decamorium* has been published, and all authors continued to list *Decamorium* as a distinct genus (e.g. Hölldobler and Wilson 1990; Bolton 1995, 2003, 2014; Robertson 2000; Hita Garcia et al. 2013).

In this study we propose *Decamorium* as a junior synonym of *Tetramorium* and lower it to the arbitrary rank of a species group. Our decision is based on a critical analysis of the diagnostic characters previously defining *Decamorium*. In addition, we revise the alpha taxonomy of the *T. decem* species group. A diagnosis of the *T. decem* species group is given together with an illustrated identification key to species on the basis of the worker caste. In addition, all members of the species group are described/re-described including diagnoses, discussions, high-quality montage images and distribution maps.

Abbreviations of depositories

The collection abbreviations follow Evenhuis (2014). The material upon which this study is based is located and/or was examined at the following institutions:

- BMNH** The Natural History Museum (British Museum, Natural History), London, U.K.
CASC California Academy of Sciences, San Francisco, U.S.A.
LACM Natural History Museum of Los Angeles County, Los Angeles, U.S.A.
MCZ Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.
MHNG Muséum d'Histoire Naturelle de la Ville de Genève, Geneva, Switzerland
MNHN Muséum National d'Histoire Naturelle, Paris, France
MSNG Museo Civico di Storia Naturale "Giacomo Doria", Genova, Italy
NHMB Naturhistorisches Museum, Basel, Switzerland
NMK National Museums of Kenya, Nairobi, Kenya
ZFMK Zoological Research Museum Alexander Koenig, Bonn, Germany

Material and methods

Most of the material examined in this study is located in the Hymenoptera collections of BMNH, CASC, MCZ, MHNG, and LACM. It includes much historical material collected prior to Bolton's review of *Decamorium* (1976), but the majority of available material has been collected over the past 20 years in a wide range of Afrotropical countries. All new type material and all imaged specimens can be uniquely identified with specimen-level codes affixed to each pin (e.g. CASENT0103295). In the descriptions presented we list all available specimen-level codes for the type series. It should be noted, however, that the number of stated paratype or syntype workers does not nec-

essarily match the number of listed specimen-level codes because pins can sometimes hold more than one specimen, especially for older species. Digital colour montage images were created using a JVC KY-F75 digital camera and Syncroscopy Auto-Montage software (version 5.0), or a Leica DFC 425 camera in combination with the Leica Application Suite software (version 3.8). All images presented are available online and can be seen on AntWeb (<http://www.antweb.org>). The distribution maps we provide (Figs 61–66) were generated with the R software (R Core Team 2014). We measured 83 workers with a Leica MZ 12.5 equipped with an orthogonal pair of micrometers at a magnification of 100×. Measurements and indices are presented as minimum and maximum values with arithmetic means in parentheses. In addition, all measurements are expressed in mm to two decimal places. The following measurements and indices used in this study follow Hita Garcia and Fisher (2011, 2012a, 2012b, 2013):

- HL** Head length: maximum distance from the midpoint of the anterior clypeal margin to the midpoint of the posterior margin of head, measured in full-face view. Impressions on the anterior clypeal margin and the posterior head margin reduce head length.
- HW** Head width: width of the head directly behind the eyes measured in full-face view.
- SL** Scape length: maximum scape length excluding basal condyle and neck.
- EL** Eye length: maximum diameter of compound eye measured in oblique lateral view.
- PW** Pronotal width: maximum width of the pronotum measured in dorsal view.
- WL** Weber's length: diagonal length of the mesosoma in lateral view from the posteroventral margin of propodeal lobe to the anterior-most point of pronotal slope, excluding the neck.
- PSL** Propodeal spine length: the tip of the measured spine, its base, and the centre of the propodeal concavity between the spines must all be in focus. Using a dual-axis micrometer the spine length is measured from the tip of the spine to a virtual point at its base where the spine axis meets orthogonally with a line leading to the median point of the concavity.
- PTH** Petiolar node height: maximum height of the petiolar node measured in lateral view from the highest (median) point of the node to the ventral outline. The measuring line is placed at an orthogonal angle to the ventral outline of the node.
- PTL** Petiolar node length: maximum length of the dorsal face of the petiolar node from the anterodorsal to the posterodorsal angle, measured in dorsal view excluding the peduncle.
- PTW** Petiolar node width: maximum width of the dorsal face of the petiolar node measured in dorsal view.
- PPH** Postpetiole height: maximum height of the postpetiole measured in lateral view from the highest (median) point of the node to the ventral outline. The measuring line is placed at an orthogonal angle to the ventral outline of the node.
- PPL** Postpetiole length: maximum length of the postpetiole measured in dorsal view.
- PPW** Postpetiole width: maximum width of the postpetiole measured in dorsal view.
- OI** Ocular index: $EL / HW * 100$

CI	Cephalic index: $HW / HL * 100$
SI	Scape index: $SL / HW * 100$
DMI	Dorsal mesosoma index: $PW / WL * 100$
LMI	Lateral mesosoma index: $PH / WL * 100$
PSLI	Propodeal spine index: $PSL / HL * 100$
PeNI	Petiolar node index: $PTW / PW * 100$
LPeI	Lateral petiole index: $PTL / PTH * 100$
DPeI	Dorsal petiole index: $PTW / PTL * 100$
PpNI	Postpetiolar node index: $PPW / PW * 100$
LPpI	Lateral postpetiole index: $PPL / PPH * 100$
DPpI	Dorsal postpetiole index: $PPW / PPL * 100$
PPI	Postpetiole index: $PPW / PTW * 100$

Pubescence and pilosity are often of high diagnostic value within the genus *Tetramorium* (e.g. Bolton 1976, 1980, 1985; Hita Garcia et al. 2010; Hita Garcia and Fisher 2012a, 2012b). The varying degree of inclination of pilosity is particularly important for the diagnosis of groups or species. In this context we use the terms “erect”, “suberect”, “subdecumbent”, “decumbent”, and “appressed” following Wilson (1955). The terminology used for the description of surface sculpturing follows Harris (1979) and Bolton (1980).

Results

Tetramorium Mayr

Tetramorium Mayr, 1855: 423. Type species: *Formica caespitum*, by subsequent designation of Girard 1879: 1016.

Tetrogmus Roger, 1857: 10. Type species: *Tetrogmus caldarius*, by monotypy. [*Tetrogmus* junior synonym of *Tetramorium*: Roger 1862: 297; Bolton 1976: 359; confirmed here.]

Xiphomyrmex Forel, 1887: 385 [as subgenus of *Tetramorium*]. Type species: *Tetramorium* (*Xiphomyrmex*) *kelleri*, by subsequent designation of Wheeler, W.M. 1911: 175. [*Xiphomyrmex* junior synonym of *Tetramorium*: Bingham 1903: 175; Bolton 1976: 359; Bolton 1980: 195; Bolton 1994: 106; Bolton 2014; confirmed here].

Triglyphothrix Forel, 1890: cvi. Type species: *Triglyphothrix walshi*, by monotypy. [*Triglyphothrix* junior synonym of *Tetramorium*: Bolton 1985: 247; confirmed here.]

Atopula Emery, 1912: 104. Type species: *Atopomyrmex nodifer*, by original designation. [*Atopula* junior synonym of *Tetramorium*: Bolton 1976: 359; Bolton 1980: 195; Bolton 1994: 106; confirmed here.]

Decamorium Forel, 1913a: 121 [as subgenus of *Tetramorium*]. Type species: *Tetramorium* (*Decamorium*) *decem*, by monotypy. [*Decamorium* raised to genus: Emery 1914: 42; Wheeler W.M. 1922: 664, 906.] **Syn. n.**

Macromischoides Wheeler, W.M. 1920: 53. Type species: *Macromischa aculeata*, by original designation. [*Macromichoides* Santschi, 1924: 206, incorrect subsequent spelling.] [*Macromischoides* junior synonym of *Tetramorium*: Bolton 1976: 359; Bolton 1980: 196, confirmed here.]

Lobomyrmex Kratochvíl, 1941: 84 [as subgenus of *Tetramorium*]. Type species: *Tetramorium (Lobomyrmex) ferox silhavyi* (junior synonym of *Tetramorium ferox*), by monotypy. [*Lobomyrmex* junior synonym of *Tetramorium*: Bolton 1976: 359; Bolton 1980: 196; confirmed here.]

Sulcomyrmex Kratochvíl, 1941: 84 [as subgenus of *Tetramorium*]. Unavailable name. Proposed without designation of type species and therefore unavailable. Species included by Kratochvíl (1941) are all referable to *Tetramorium*: Bolton 1976: 359.

Apomyrmex Calilung, 2000: 66. Type species: *Apomyrmex manobo*, by original designation. [*Apomyrmex* junior synonym of *Tetramorium*: Bolton 2003: 227, 269; confirmed here.]

***Decamorium* Forel—a junior synonym of *Tetramorium* Mayr**

As outlined in the introduction, in the past various authors expressed very different opinions about the status of *Decamorium*. After examination of all available material and dissemination of all previous literature, we have come to the conclusion that *Decamorium* is best treated as a junior synonym of *Tetramorium*. Our reasons are summarised below:

1. Antennomere count

As outlined above, the antennomere count was the main diagnostic character qualifying *Decamorium* as a genus (Emery 1924; Bolton 1976). Antennomere count has traditionally been considered a very good diagnostic character for separating closely related genera. Yet over the past few decades it has become apparent that the antennal count can vary within a genus, sometimes significantly. Some examples include the genera *Carebara* Westwood with eight to eleven segments (Fernandez 2004), *Temnothorax* Mayr which typically has twelve segments, rarely eleven (Bolton 2003; Radchenko 2004), *Cardiocondyla* Emery with eleven and twelve segments (Seifert 2003), or *Pheidole* with nine to twelve (Bolton 2003). Also, in some African species of *Carebara* the major workers always have one antennal segment more than the minor workers. Furthermore, subgroups of the same genus often have been placed in different genera in the past due to varying antennomere counts. One good example is *Myrmelachista* Roger outlined in Longino (2006). It was originally described by Roger (1863) as two genera: *Decamera* Roger (a junior homonym of a beetle genus and replaced by the name *Hincksidris* Donisthorpe) having ten-segmented antennae, and *Myrmelachista* having eleven-segmented antennae. This division turned out to be incorrect, and Brown (1973) and Snelling and Hunt (1976) formally synonymised them more than a century later.

In what is now considered to be *Tetramorium* one can find eleven-segmented and twelve-segmented antennae throughout all biogeographical regions, even though most of

these forms were previously separated into *Xiphomyrmex* (11-segmented antennae) and *Tetramorium* (12-segmented antennae). Bolton (1976) provided evidence based on sting appendage types showing that this separation was an artificial one, and consequently synonymised *Xiphomyrmex* under *Tetramorium*. Based on this intrageneric variation in antennal segmentation, we accept that a small and highly specialised African species group within *Tetramorium* could have an even more reduced count of ten antennal segments.

This is further supported by the presence of a very small species from India that possesses 10-segmented antennae: *T. decamerum* (Forel). This species was treated as *Triglyphothrix* by Bolton (1976), thus not taken into consideration as a *Tetramorium*. The later synonymisation of *Triglyphothrix* under *Tetramorium* Bolton (1985) provided a “genuine” *Tetramorium* with 10-segmented antennae. Consequently, this character is not unique to *Decamerium*, but already present in *Tetramorium*.

2. Clypeal shield

The reduced clypeal shield seen in *Decamerium* (Fig. 1A) is not unique to its species. Within the tropical *Tetramorium* fauna most species have a very well-developed and clearly distinctive clypeal shield (Figs 1F, 1G, 1H, 1I), but there are a number of species, such as *T. nodiferum* (Emery) (Fig. 1B), *T. simulator* Arnold (Fig. 1C), *T. aculeatum* (Mayr) (Fig. 1D), or *T. anodontion* Bolton (Fig. 1E), in which this shield is much less pronounced or almost reduced. The clypeal shield generally varies from species to species in its height and the sharpness of its dorsal edge. When the development of this character

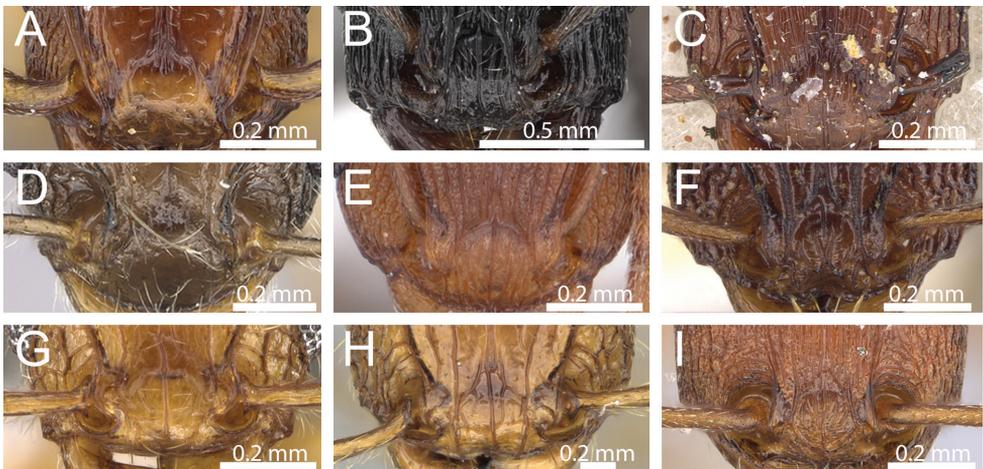


Figure 1. Anterior head showing varying development of the clypeal shield. **A** *T. decem* (CASENT0914088) **B** *T. nodiferum* (CASENT0217218) **C** *T. simulator* (CASENT0914089) **D** *T. aculeatum* (CASENT0235778) **E** *T. anodontion* Bolton (CASENT0102334) **F** *T. diomandei* Bolton (CASENT0901166) **G** *T. hecate* Hita Garcia & Fisher (CASENT0248334) **H** *T. melanogyna* Mann (CASENT0199931) **I** *T. sericeiventre* (CASENT0235773).

across several hundred *Tetramorium* species is considered, *Decamorium* emerges as one extreme of a cline that ranges from almost no clypeal shield to a very sharp and high shield, such as in the members of the *T. sericeiventre* Emery species group (Fig. 11).

3. Mandibular dentition

The mandibular dentition of *Decamorium* and *Tetramorium* seemed slightly different back in 1976, but as anticipated by Bolton, it has become clear that there is much more variation within *Tetramorium*. Currently there is no significant difference in mandibular dentition between *Decamorium* and *Tetramorium*. In *Decamorium* the mandibular count consists of three apical teeth followed by a series of four or five denticles, while in *Tetramorium* there are two to three apical teeth followed by a series of three to eight denticles (Bolton 2003). Consequently, this character has no diagnostic importance in this group since the values of *Decamorium* fall well within the range of the larger *Tetramorium*.

4. *Tetramorium simulator* Arnold

If one considers the whole tribe Tetramoriini, then it becomes apparent that the specialised habitus of *Decamorium* is not unique. Several authors have stated that *Decamorium* are specialised termite hunters, and that their specialised morphology could be an adaptation to such a dangerous lifestyle (Arnold 1917; Bolton 1976; Longhurst et al. 1979). Interestingly, both Arnold (1917) in the original description and later Bolton (1980) noted the similarities in general body shape and diet between members of *Decamorium* and the species *Tetramorium simulator* from South Africa. We agree that the similarities in morphology are indeed obvious, especially in profile view (Fig. 2). However, at present it is not clear whether the shared morphology is based on a close phylogenetic relationship between *Decamorium* and *T. simulator* or a result of convergent evolution due to a similar lifestyle hunting termites. We believe the latter more likely since the twelve-segmented antennae, the much broader head, and sculptured clypeus of *T. simulator* suggest a closer relationship to another group with twelve-segmented antennae than to *Decamorium*. Therefore, we hypothesise that both have evolved from different *Tetramorium* lineages and acquired the specialised habitus independently from each other. Another remarkable aspect is the lack of a strong and sharp clypeal shield in *T. simulator*, which seems to have been reduced in a manner almost similar, though less pronounced, to *Decamorium*.

5. Male morphology

We do not intend to go into details of male morphology here, but so far there is not a single character that would separate the males of *Decamorium* from the males of



Figure 2. Head in full-face view and body in profile. **A, B** *T. decem* (CASENT0914087) **C, D** *T. simulator* (CASENT0914089).

Tetramorium; a result that agrees with Bolton's findings (1976). It should be noted, however, that *Decamorium* males are very rare, and only one specimen was available for examination (BMNH: CASENT0901037).

6. Molecular evidence

In addition to our morphological analysis above, there is also molecular evidence supporting the synonymisation of *Decamorium* under *Tetramorium*. Based on a multi-gene dataset, Ward et al. (in press) show that *Decamorium* is nested within a larger *Tetramorium* clade. However, how *Decamorium* is integrated into *Tetramorium* and to which groups/lineages it is most closely related remains unknown. Further phylogenetic/phylogenomic studies that deal with a greater number of species groups and a good proportion of species are needed to clarify relationships within the hyperdiverse *Tetramorium* and its satellite genera.

Revision of the *Tetramorium decem* species group

Synopsis of the *Tetramorium decem* species group

- Tetramorium decem* Forel, 1913a, **comb. r.**
- Tetramorium raptor* Hita Garcia, **sp. n.**
- Tetramorium uelense* Santschi, 1923, **comb. r.**
- Tetramorium ultor* Forel, 1913b, **comb. r., stat. r. & stat. n.**
- Tetramorium venator* Hita Garcia, **sp. n.**

Diagnosis of *Tetramorium decem* species group

Ten-segmented antennae; antennal scape relatively short (SI 67–76); anterior clypeal margin with distinct but often shallow impression; frontal carinae strongly developed and noticeably raised, forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and usually ventral scrobe margins; antennal scrobes very well developed, deep and usually with clearly defined margins all around, median scrobal carina absent; eyes relatively large (OI 32–40); mesosoma relatively flat, low, and elongated, margination between lateral and dorsal mesosoma moderately developed (LMI 33–38); propodeum armed with short triangular to elongate-triangular teeth (PSLI 9–19); propodeal lobes short, rounded to triangular; tibiae and femorae strongly swollen; petiolar node nodiform with moderately rounded antero- and posterodorsal margins, petiolar dorsum weakly to strongly convex, node in profile between 1.0 to 1.3 times higher than long (LPeI 77–100), node in dorsal view around 1.1 to 1.3 times longer than wide (DPeI 76–92); postpetiole in profile globular, around 1.1 to 1.4 times higher than long (LPpI 71–88); mandibles and clypeus unsculptured, smooth, and shiny; sculpture on cephalic dorsum between frontal carinae and dorsal mesosoma variable, ranging from unsculptured, smooth, and shiny to longitudinally rugose/rugulose, often punctate or puncticulate; petiole usually weakly sculptured, postpetiole unsculptured to weakly sculptured; gaster unsculptured, smooth, and shiny; pilosity greatly reduced, head with several pairs of standing hairs, mesosoma with one pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one pair; sting appendage triangular.

Taxonomic and biogeographic notes on the group

The *T. decem* species group is endemic to the Afrotropical region where it is widely distributed (Fig. 3). *Tetramorium raptor* and *T. uelense* are found in West and Central Africa and *T. venator* occurs through most of the equatorial rainforest belt from Liberia in West Africa to Western Kenya. By contrast, *T. decem* and *T. ultor* are species from eastern and southeastern Africa. Surprisingly, the group seems to be absent from South Africa based on the material available to us, but *T. decem* or *T. ultor* are likely to be found there or in neighbouring Botswana or Namibia. Furthermore, we expect the distribution ranges of *T. decem*, *T. uelense*, and perhaps *T. ultor* to expand with further ant inventory or collecting projects in Afrotropical savannahs, dry forests, and other arid habitats. These were sparsely sampled in sub-Saharan Africa in the past since most modern ant inventories have focused on rainforests (e.g. Belshaw and Bolton 1994; Watt et al. 2002; Fisher 2004; Yanoviak et al. 2007; Hita Garcia et al. 2009), whereas only a few studies have examined ant faunas from drier localities (e.g. Robertson 1999, 2002; Braet and Taylor 2008).

The separation of the *T. decem* species group from all other *Tetramorium* species groups is straightforward and easy. So far, only the members of the *T. decem* group have

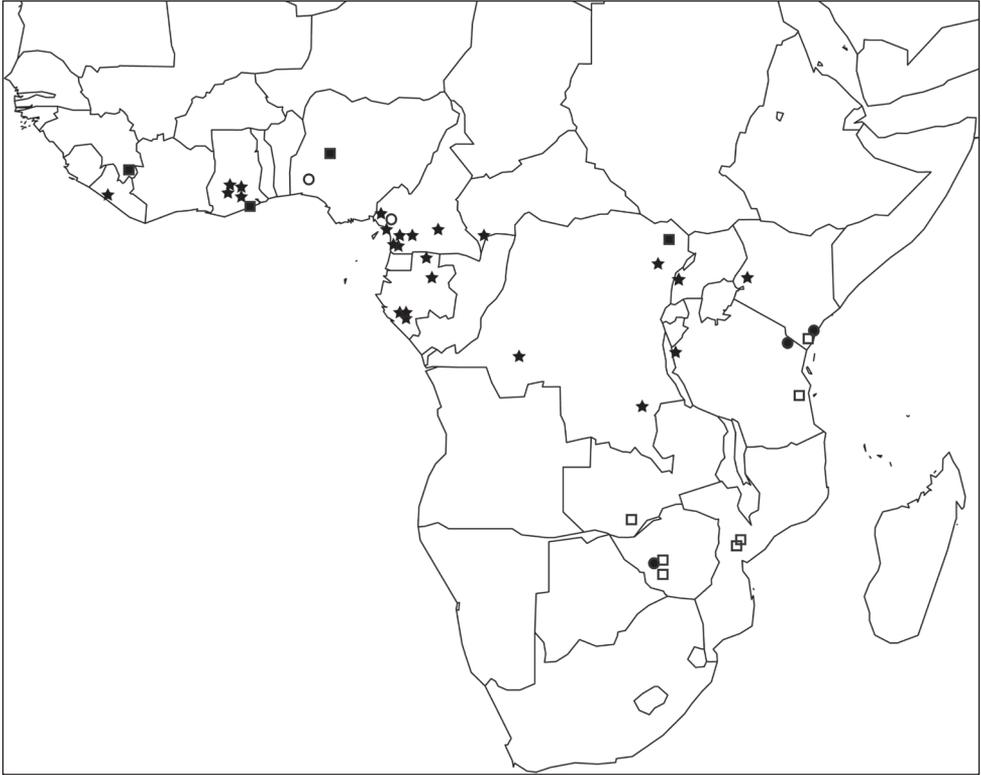


Figure 3. Map of sub-Saharan Africa showing the known distribution ranges of the five members of the *T. decem* species group: *T. decem* (filled circle), *T. raptor* (empty circle), *T. uelense* (filled square), *T. ultor* (empty square), and *T. venator* (star).

ten-segmented antennae, whereas all other Afrotropical *Tetramorium* have either eleven or twelve. Consequently, the *T. decem* species group is unlikely to be confused with another Afrotropical group. The morphology of the five species of the group is very uniform, likely due to their strongly specialised lifestyle, which makes the taxonomy of the group challenging at first sight. However, good diagnostic characters separate them fairly well from each other, especially eye size, propodeal spine/teeth length, petiolar node shape, mesosomal sculpture, and body colouration. These characters are remarkably consistent within each species throughout its whole distribution, as are the species-specific habitat preferences.

Identification key for *T. decem* species group (workers)

- 1 Dorsum of promesonotum with conspicuous longitudinally rugose/rugulose sculpture (Fig. 4A, B).....2
- Dorsum of promesonotum unsculptured, smooth, and usually very shiny (Fig. 4C, D).....3

- 2 Slightly smaller species (WL 0.88–0.93); propodeum armed with shorter, triangular, and acute teeth (PSLI 10–11); dorsum of promesonotum longitudinally rugulose with very little ground sculpture, lateral pronotum mostly unsculptured and shiny, only dorsally longitudinally rugulose; generally of uniform dark brown colour; rainforest species (Fig. 5A, B) [Cameroon, Nigeria] *T. raptor*
- Slightly larger species (WL 0.98–1.06); propodeum armed with longer, triangular to elongate-triangular, and acute teeth (PSLI 16–18); dorsum of promesonotum and lateral pronotum strongly longitudinally rugose with distinct punctate ground sculpture; strongly bicoloured species with dark brown or black gaster contrasting with light brown to reddish brown on remainder of body; savannah species (Fig. 5C, D) [Cameroon, Ghana, Guinea, Nigeria, and Republic of the Congo]..... *T. uelense*
- 3 Generally larger species (WL 1.02–1.16); propodeal teeth relatively longer (PSLI 17–19); petiolar node in profile relatively higher, in profile 1.2 to 1.3 times higher than long (LPeI 77–82); strongly bicoloured species with dark brown or black gaster contrasting with light brown to reddish brown remainder of body (Fig. 6A) [Kenya, Tanzania, and Zimbabwe] *T. decem*
- Generally smaller species (WL 0.85–0.98); propodeal teeth relatively shorter (PSLI 9–13); petiolar node relatively lower, in profile around 1.0 to 1.2 times higher than long (LPeI 86–100); usually of uniform brown colour, if bicoloured, then only slightly so and never as well developed as above (Fig. 6B)..... **4**
- 4 Smaller eyes (OI 33–36); body colouration uniformly light brown to chestnut brown (Fig. 7A, B) [Kenya, Mozambique, Tanzania, Zambia, and Zimbabwe] *T. ultor*
- Larger eyes (OI 37–40); body colouration uniformly dark brown to black, always darker than above (Fig. 7C, D) [Central African Republic, Cameroon, Democratic Republic of Congo, Gabon, Ghana, Kenya, Liberia, Tanzania, Uganda]..... *T. venator*

***Tetramorium decem* Forel, 1913a, comb. n.**

Figs 1A, 2A, 2B, 3, 6A, 8

Tetramorium (*Decamorium*) *decem* Forel, 1913a: 121. [Combination in *Decamorium* by Wheeler 1922: 906; senior synonym of *Decamorium ultor* by Bolton 1976: 298.]

Type material. **Lectotype** [designated here], pinned worker, ZIMBABWE, Redbank, 19.98333 S, 28.37759 E, 7.IV.1912 (*G. Arnold*) (MHNG: CASENT0909196) [examined]. **Paralectotypes** [designated here], seven pinned workers with same data as lectotype (BMNH: CASENT0901035; MHNG: CASENT0248316; MSNG: CASENT0904789) [examined].

[Note: the GPS data of the type locality was not provided by the locality label or the original description. The data presented above is based on our own geo-referencing

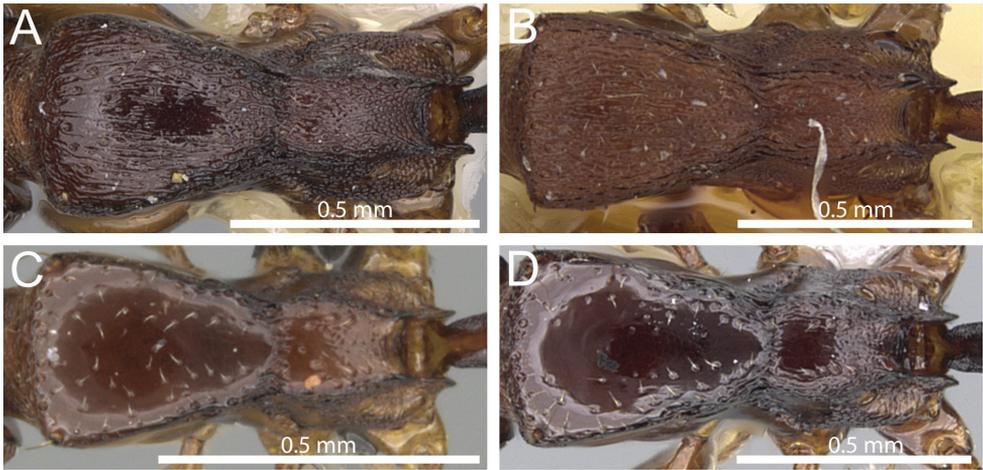


Figure 4. Mesosoma in dorsal view. **A** *T. raptor* (CASENT0195628) **B** *T. uelense* (CASENT0914084) **C** *T. ultor* (CASENT0235465) **D** *T. venator* (CASENT0401714).

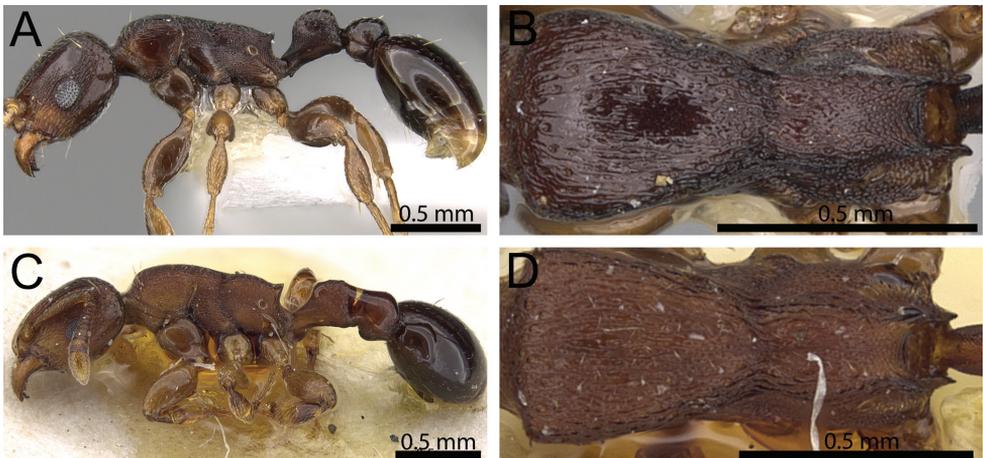


Figure 5. Body in profile and mesosoma in dorsal view. **A, B** *T. raptor* (CASENT0280848) **C, D** *T. uelense* (CASENT0914084).

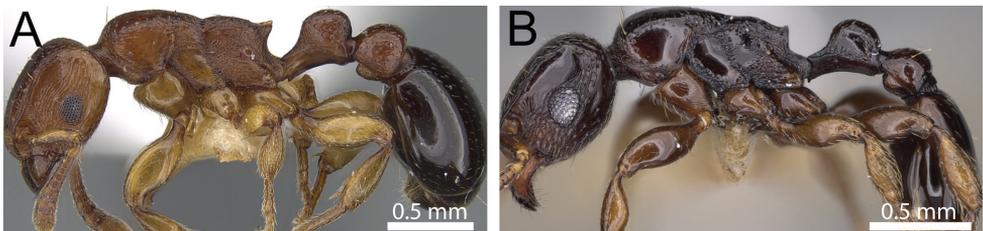


Figure 6. Body in profile. **A** *T. decem* (CASENT0914088) **B** *T. venator* (CASENT0195574).

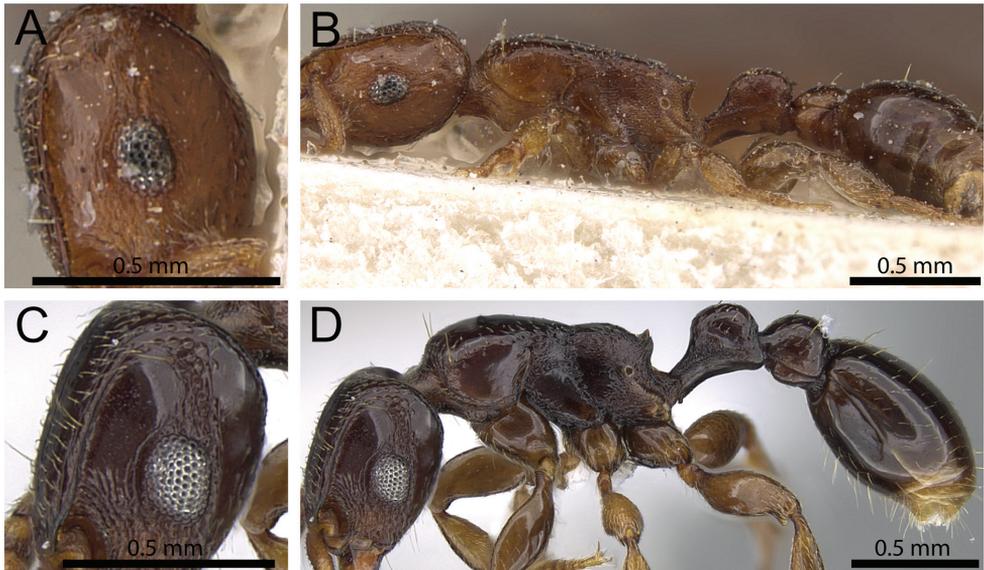


Figure 7. Head and body in profile. **A, B** *T. ultor* (CASENT0235465) **C, D** *T. venator* (CASENT0401714).

of the town of Redbank located in the Matabeleland North Province. Consequently, the location should be considered as an approximation and not the exact position of the type locality.]

Non-type material. KENYA: Coastal Province, Malindi District, Arabuko Sokoke Forest, 3.28 S, 39.97 E, 75 m, Brachystegia forest, 26.V.2001 (*R.R. Snelling & D.J. Martins*); Coastal Province, Malindi District, Arabuko Sokoke Forest, 3.32111 S, 39.92944 E, ca. 50 m, VI.2009 (*F. Hita Garcia & G. Fischer*); TANZANIA: Mkomazi Game Reserve, Ibaya, 3.96667 S, 37.8 E, in burnt grassland, 19.–20.XI.1994 (*A. Russel-Smith*).

Diagnosis. *Tetramorium decem* can be recognised by the following combination of characters: relatively larger species (HW 0.59–0.62; WL 1.02–1.16); propodeal teeth relatively longer (PSLI 17–19); petiolar node in profile around 1.2 to 1.3 times higher than long (LPel 77–82); dorsum of promesonotum unsculptured, smooth, and very shiny; strongly bicoloured species with dark brown or black gaster contrasting with light brown to reddish brown remainder of body.

Worker measurements (N=15). HL 0.71–0.74 (0.72); HW 0.59–0.62 (0.60); SL 0.42–0.45 (0.43); EL 0.19–0.21 (0.20); PH 0.33–0.37 (0.35); PW 0.47–0.50 (0.48); WL 1.02–1.16 (1.06); PSL 0.12–0.14 (0.13); PTL 0.25–0.27 (0.26); PTH 0.31–0.34 (0.33); PTW 0.22–0.24 (0.23); PPL 0.24–0.27 (0.25); PPH 0.32–0.36 (0.34); PPW 0.32–0.36 (0.34); CI 83–85 (84); SI 70–76 (72); OI 32–34 (33); DMI 41–47 (45); LMI 32–34 (33); PSLI 17–19 (18); PeNI 46–51 (48); LPel 77–82 (80); DPel 85–92 (88); PpNI 67–76 (70); LPpI 71–77 (75); DPpI 128–138 (133); PPI 143–149 (147).

Worker description. Head much longer than wide (CI 83–85); posterior head margin weakly concave. Anterior clypeal margin with distinct, but often shallow median impression. Frontal carinae strongly developed and noticeably raised forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and parts of ventral scrobe margins; antennal scrobes very well developed, deep and with clearly defined margins, but ventral margin less strongly developed, median scrobal carina absent. Antennal scapes short, not reaching posterior head margin (SI 70–76). Eyes very large (OI 32–34). Mesosomal outline in profile flat to weakly convex, relatively low and elongate (LMI 32–34), moderately to strongly marginate from lateral to dorsal mesosoma; promesonotal suture absent; metanotal groove present, distinct, and clearly impressed. Propodeal spines short, elongate-triangular, and moderately acute (PSLI 17–19), propodeal lobes short, triangular, and usually blunt, always significantly shorter than propodeal spines. Tibiae and femorae strongly swollen. Petiolar node nodiform with moderately rounded antero- and posterodorsal margins, around 1.2 to 1.3 times higher than long (LPeI 77–82), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about the same height, petiolar dorsum clearly convex; node in dorsal view between 1.1 to 1.2 times longer than wide (DPeI 85–92), in dorsal view pronotum around 2.0 to 2.2 times wider than petiolar node (PeNI 46–51). Postpetiole in profile globular to subglobular, approximately 1.3 to 1.4 times higher than long (LPpI 71–77); in dorsal view around 1.3 to 1.4 times wider than long (DPpI 128–138), pronotum between 1.3 to 1.5 times wider than postpetiole (PpNI 67–76). Postpetiole in profile usually appearing less voluminous than petiolar node, postpetiole in dorsal view around 1.4 to 1.5 times wider than petiolar node (PPI 143–149). Mandibles and clypeus usually fully unsculptured, smooth, and shining, mandibles sometimes with few traces of rugulae apically; cephalic dorsum between frontal carinae mostly unsculptured and shiny, median ruga present and distinct, cephalic dorsum also punctulate to punctate throughout its length, posteriorly close to posterior head margin especially pronounced; scrobal area partly unsculptured, smooth and shiny and partly merging with surrounding rugose sculpture on sides of head. Ground sculpture on head usually weak to absent. Dorsum of mesosoma mostly unsculptured, smooth and shiny with scattered punctures, rarely with few traces of rugulae; lateral mesosoma longitudinally rugose and very conspicuously reticulate-punctate except for mostly unsculptured lateral pronotum and katapisternum. Forecoxae unsculptured, smooth, and shining. Petiolar node and postpetiole superficially longitudinally rugulose or irregularly rugulose superimposed on conspicuous but relatively weak reticulate-punctate ground sculpture. Mesosoma and waist segments appearing mostly matt. First gastral tergite unsculptured, smooth, and shiny. Pilosity and pubescence greatly reduced: head with few pairs of moderately long, standing hairs, anterior pronotum with one long pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one long pair; appressed pubescence present everywhere on body, but noticeable only on antennae, cephalic dorsum, legs, and first gastral

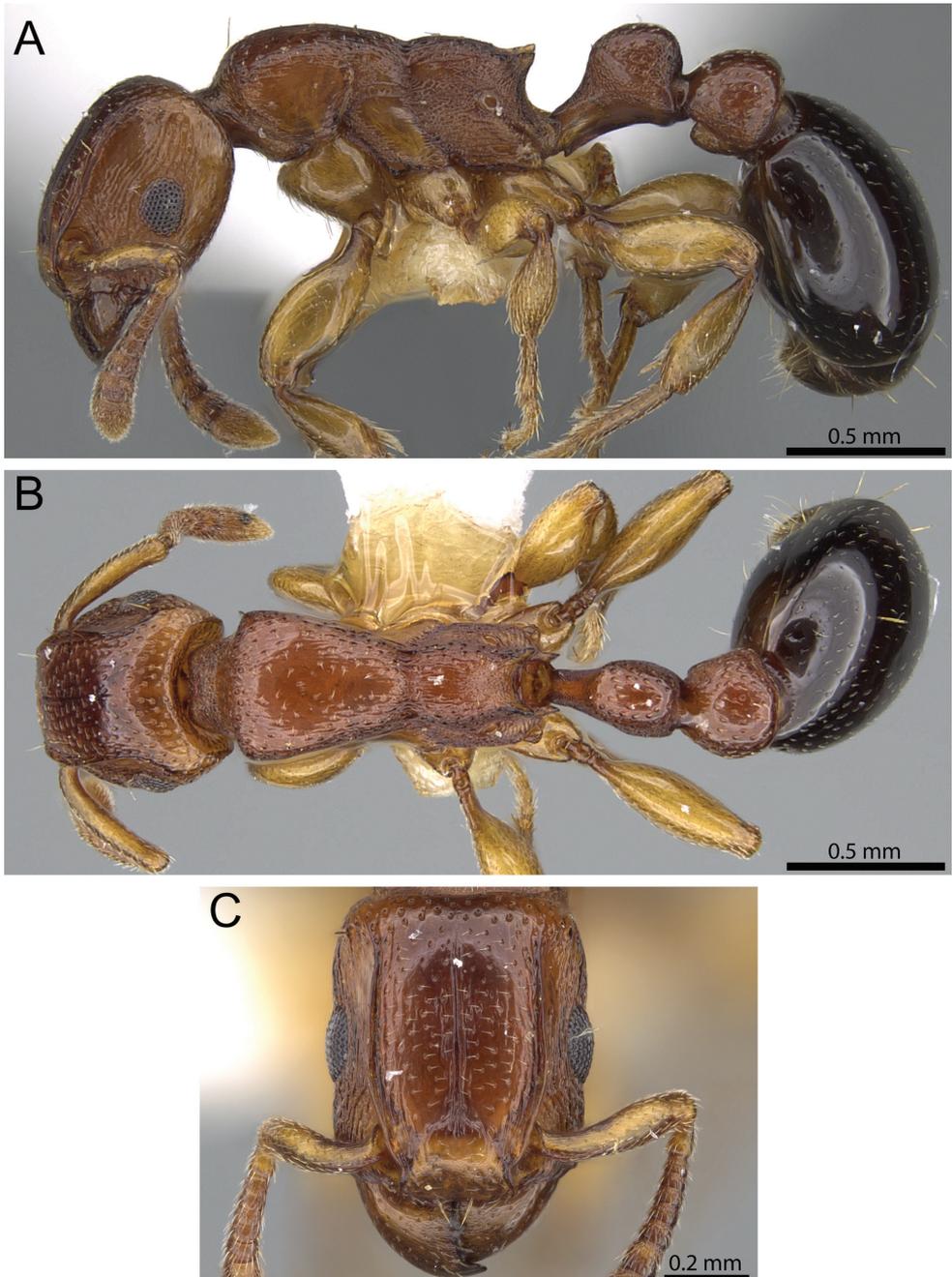


Figure 8. *T. decem* non-type worker (CASENT0914088). **A** Body in profile **B** Body in dorsal view **C** Head in full-face view.

tergite. Anterior edges of antennal scapes and dorsal (outer) surfaces of hind tibiae with appressed hairs. Body strongly bicoloured with dark brown to black gaster contrasting with light brown to reddish brown remainder.

Distribution and biology. The distribution range of *T. decem* is far smaller than previously thought (Fig. 3). Indeed, most of the material listed in the literature as *T. decem* or labelled as such in museum collections turned out to be either *T. ultor* or *T. venator*, while only a few collections proved to be genuine *T. decem*. Based on the re-defined species definition, *T. decem* is only known from the type locality in Zimbabwe and two additional localities in East Africa: Arabuko Sokoke in Kenya and Mkomazi in Tanzania. Nevertheless, if more extensive sampling efforts are undertaken in East Africa, *T. decem* is likely to be found in more localities in Kenya, Tanzania, and Zimbabwe. Like *T. uelense* and *T. ultor*, *T. decem* prefers arid habitats, such as savannah and woodland. Based on Arnold (1917) and the collection label from some material from Arabuko Sokoke, *T. decem* nests in sandy soil. The diet consists of termites, as with most other members of the species group.

Discussion. *Tetramorium decem* is the core species of the group, and was the type species for the description of the subgenus *Decamorium* by Forel (1913a). It is perhaps the most conspicuous species of the group. Its bicolouration, larger size, lack of sculpture on the mesosomal dorsum, and a higher petiolar node render it immediately recognisable. The mostly unsculptured, smooth and shiny mesosomal dorsum distinguishes *T. decem* from *T. raptor* and *T. uelense*, in which the dorsum of the mesosoma is clearly longitudinally rugose/rugulose. *Tetramorium ultor* and *T. venator* both share the lack of sculpture on the mesosomal dorsum with *T. decem*, but can still be easily separated from the latter. *Tetramorium decem* is generally larger in size (WL 1.02–1.16), has longer propodeal spines (PSLI 17–19) and is also conspicuously bicoloured, whereas *T. ultor* and *T. venator* are smaller species (WL 0.85–0.98) with significantly shorter propodeal teeth (PSLI 9–13) and a more uniform brown to black body colouration. In addition, *T. decem* also has a higher petiolar node, in profile around 1.2 to 1.3 times higher than long (LPeI 77–82), compared to the other two, in which the node in profile is only around 1.0 to 1.2 times higher than long (LPeI 86–100). The species that appears to be morphologically closest to *T. decem* is *T. uelense*. Both species share the large body, bicolouration, and preference for arid habitats. However, in addition to the sculpture on the mesosoma, *T. uelense* also has a lower petiolar node, in profile around 1.1 times higher than long (LPeI 88–93). Another character that is shared between *T. decem* and *T. uelense* but absent in the other species of the group is the development of the ventral margin of the antennal scrobe. In *T. raptor*, *T. ultor*, and *T. venator* the margin is clearly and well defined, while in *T. decem* and *T. uelense* it is less so and merges more with the surrounding rugose sculpture.

Variation. Based on the available material we did not observe any significant form of intraspecific variation in *T. decem*.

***Tetramorium raptor* Hita Garcia, sp. n.**

<http://zoobank.org/6A9F212B-8460-41C0-9F8C-792D9A4780C4>

http://species-id.net/wiki/Tetramorium_raptor

Figs 3, 4A, 5, 9

Type material. **Holotype**, pinned worker, CAMEROON, Sud-Ouest, Bakundu, 4.49222 N, 9.375 E, collection code ANTC27989, 8.XI.1990 (*A. Dejean*) (BMNH: CASENT0195628). **Paratypes**, 14 pinned workers with same data as holotype (BMNH: CASENT0195581; CASENT0195630; CASENT0195631; CASC: CASENT0195633; CASENT0195634; LACM: LACM_ENT_323500; MCZ: CASENT0195628; ZFMK: CASENT0195632).

[Note: the GPS data of the type locality was not provided by the locality label. The data presented above is based on our own geo-referencing of the Bakundu Forest located in the province Sud-Ouest. Consequently, it should be considered an approximation and not the exact position of the type locality.]

Non-type material. CAMEROON: Sud-Ouest, Bakundu, 4.49222 N, 9.375 E, 8.XI.1990 (*A. Dejean*); NIGERIA: Gambari, 10.VI.1969 (*B. Bolton*); Gambari, C.R.I.N., 17.VI.1975 (*B. Taylor*).

Diagnosis. *Tetramorium raptor* is easily recognisable within the group on the basis of the following combination of characters: relatively smaller species (WL 0.88–0.93); very large eyes (OI 35); propodeum armed with very short triangular teeth (PSLI 10–11); petiolar node in profile around 1.1 times higher than long (LPeI 89–93); dorsum of mesosoma with longitudinally rugulose sculpture; body uniformly dark brown, appendages of lighter brown.

Worker measurements (N=12). HL 0.64–0.68 (0.67); HW 0.53–0.56 (0.54); SL 0.37–0.41 (0.39); EL 0.19–0.20 (0.XX); PH 0.31–0.34 (0.33); PW 0.40–0.43 (0.41); WL 0.88–0.93 (0.91); PSL 0.07–0.08 (0.07); PTL 0.23–0.25 (0.24); PTH 0.26–0.28 (0.27); PTW 0.19–0.21 (0.20); PPL 0.21–0.24 (0.22); PPH 0.25–0.28 (0.27); PPW 0.26–0.30 (0.28); CI 80–83 (82); SI 70–73 (72); OI 35; DMI 44–47 (45); LMI 35–37 (36); PSLI 10–11 (11); PeNI 47–51 (48); LPeI 89–93 (90); DPeI 80–85 (82); PpNI 64–70 (68); LPPi 81–88 (85); DPPi 123–130 (125); PPI 137–150 (142).

Worker description. Head much longer than wide (CI 80–83); posterior head margin weakly concave. Anterior clypeal margin with distinct but often shallow median impression. Frontal carinae strongly developed and noticeably raised forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and ventral scrobe margins; antennal scrobes very well developed, deep and with clearly defined margins all around, median scrobal carina absent. Antennal scapes short, far from reaching posterior head margin (SI 70–73). Eyes relatively large (OI 35). Mesosomal outline in profile relatively flat, elongate and low (LMI 35–37), moderately to strongly marginate from lateral to dorsal mesosoma; promesonotal suture absent; metanotal groove present and conspicuous, but relatively shallow. Propodeum armed with short, triangular, and usually acute teeth (PSLI 10–11), propodeal lobes short, well round-

ed, and usually larger than propodeal teeth. Petiolar node nodiform with moderately rounded antero- and posterodorsal margins, in profile around 1.1 times higher than long (LPeI 89–93), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height and equally angled, petiolar dorsum weakly convex; node in dorsal view around 1.2 to 1.3 times longer than wide (DPeI 80–85), in dorsal view pronotum around 2.0 to 2.2 times wider than petiolar node (PeNI 47–51). Postpetiole in profile globular, approximately 1.1 to 1.2 times higher than long (LPpI 81–88); in dorsal view around 1.2 and 1.3 times wider than long (DPpI 123–130), pronotum around 1.4 to 1.6 times wider than postpetiole (PpNI 64–70). Postpetiole in profile appearing less voluminous than petiolar node, postpetiole in dorsal view around 1.4 to 1.5 times wider than petiolar node (PPI 137–150). Mandibles and clypeus unsculptured, smooth, and shining; cephalic dorsum between frontal carinae with fine irregularly longitudinally rugulose sculpture, rugulae running from posterior clypeal margin to posterior head margin, often interrupted or meandering, rarely with cross-meshes, cephalic dorsum also punctulate to punctate throughout its length, otherwise without ground sculptured; scrobal area partly unsculptured, smooth and shiny and partly strongly reticulate-punctate; lateral head mainly reticulate-rugose with weak to moderately well developed punctate ground sculpture. Dorsum of mesosoma densely longitudinally rugulose, anteriorly without much ground sculpture, posteriorly on top of strong reticulate-punctate ground sculpture; lateral pronotum and katepisternum mostly unsculptured, smooth, and shiny, remainder of lateral mesosoma irregularly rugose and very conspicuously reticulate-punctate. Forecoxae unsculptured, smooth, and shining. Petiolar node laterally reticulate-punctate, dorsum of node mostly unsculptured, smooth, and shiny; postpetiole mostly unsculptured, smooth, and shiny with scattered punctures. First gastral tergite unsculptured, smooth, and shiny. Pilosity and pubescence greatly reduced: head with few pairs of moderately long, standing hairs, anterior pronotum with one long pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one long pair; appressed pubescence present everywhere on body, but noticeable only on antennae, cephalic dorsum, legs, and first gastral tergite. Anterior edges of antennal scapes and dorsal (outer) surfaces of hind tibiae with appressed hairs. Body uniformly dark brown to black, appendages of lighter brown.

Etymology. The name of the new species is Latin and means “thief, robber, or plunderer”. It refers to the predaceous lifestyle of *T. raptor*. The species epithet is a nominative noun, and thus invariant.

Distribution and biology. *Tetramorium raptor* is currently only known from the type locality Bakundu in the southeast of Cameroon and from Gambari in southwestern Nigeria (Fig. 3). Based on the minimal collection label data, *T. raptor* lives in rainforest leaf litter.

Discussion. *Tetramorium raptor* is an easily distinguishable member of the *T. decem* group, but was not recognised until this study. Indeed, all known material was collected in 1969 and 1990, but labelled as *T. uelense* on the basis of the distinctive sculpture on the mesosomal dorsum. The presence of conspicuous, longitudinally rugulose sculpture on the dorsum of the promesonotum distinguishes it from *T. decem*, *T.*

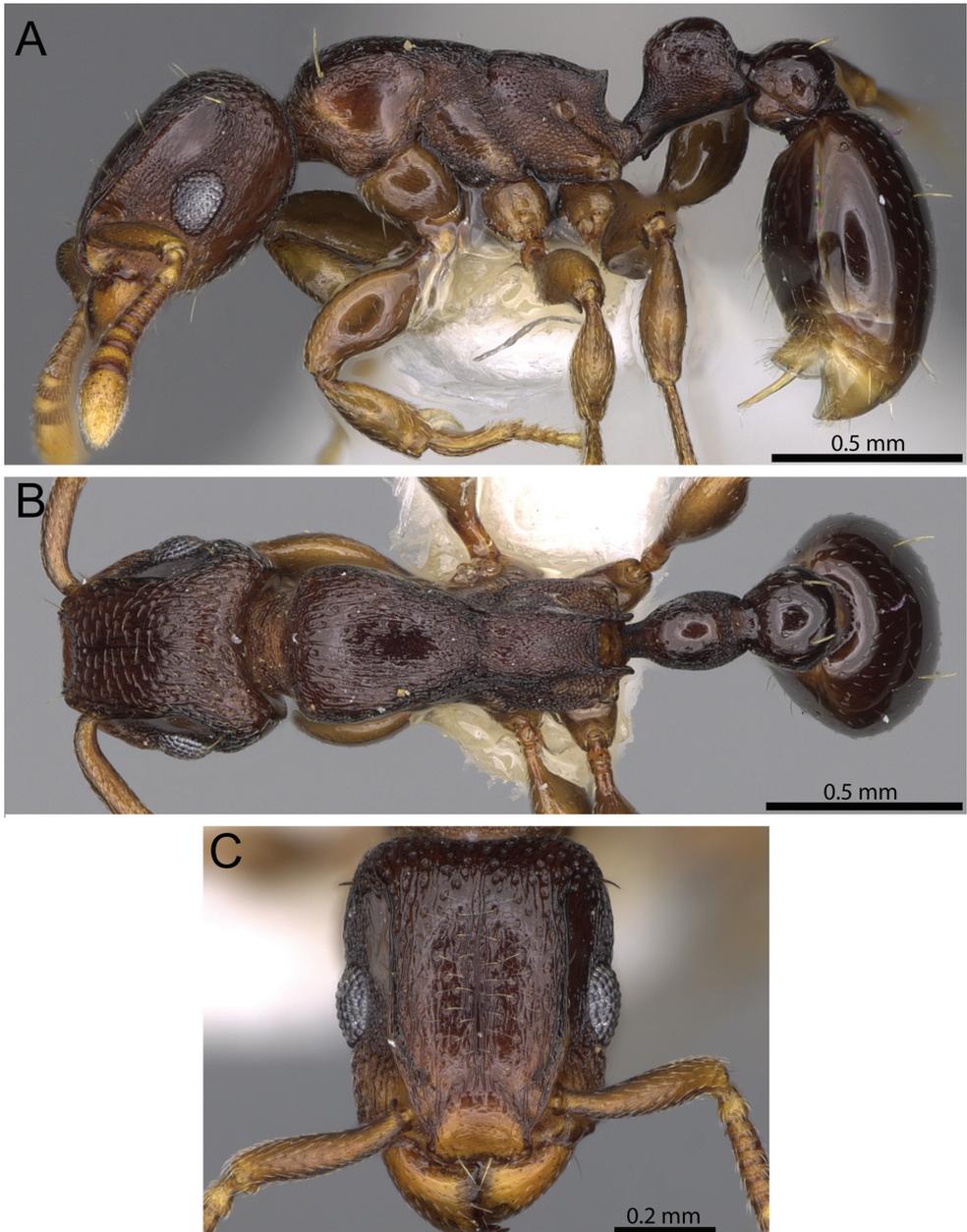


Figure 9. *T. raptor* holotype worker (CASENT0195628). **A** Body in profile **B** Body in dorsal view **C** Head in full-face view.

ultor, or *T. venator*, since the latter three all lack sculpture on the promesonotal dorsum. *Tetramorium uelense*, however, shares the presence of sculpture on the mesosomal dorsum with *T. raptor*, which led to the abovementioned misidentifications. Nevertheless, careful examination of all material previously listed as *T. uelense* revealed the presence

of two morphologically and ecologically different species. The most obvious differences are body size and colour. *Tetramorium uelense* is strongly bicoloured and larger (WL 0.98–1.06) than the smaller and uniformly-coloured *T. raptor* (WL 0.88–0.93). The latter also has shorter propodeal teeth (PSLI 10–11) than *T. uelense* (PSLI 16–18). Furthermore, *T. raptor* possesses a longitudinally rugulose promesonotal dorsum with very little ground sculpture and a mostly unsculptured and shiny lateral pronotum, whereas *T. uelense* has a promesonotal dorsum that is longitudinally rugose with distinct punctate ground sculpture and a lateral pronotum that is conspicuously rugose with prominent ground sculpture. In addition, both species also differ in habitat choice, as *Tetramorium uelense* seems to prefer savannah while *T. raptor* lives in rainforest.

Variation. Based on material from the two known localities, there is no intraspecific variation in *T. raptor*.

***Tetramorium uelense* Santschi, 1923, comb. n.**

Figs 3, 4B, 5C, 5D, 10

Tetramorium (Decamorium) decem uelense Santschi, 1923: 285. [Combination in *Decamorium* and raised to species by Bolton 1976: 298.]

Decamorium decem nimba Bernard, 1953: 250. [Junior synonym of *T. uelense* by Bolton 1976: 298; here confirmed.]

Type material. Of *uelense*: lectotype, pinned worker, D. R. CONGO (Congo belge), Uelé, Vankerhovenville, 3.0 N, 29.5 E (*Degreeff*) (NHMB: CASENT0906826) [examined]. **Paralectotype**, pinned queen with same data as lectotype (MRAC) [not examined].

Of *nimba*: holotype, pinned worker, GUINEA, Kéoulenta, 7.714053 N, 8.331786 W, St. 1 Savane, (MNHN: CASENT0914084) [examined].

[Note: GPS data for neither of the type localities was included on the locality labels or the original descriptions. The data presented above is based on our own georeferencing of Vankerhovenville located in Province Orientale and Kéoulenta located in the Nzérékoré Region. Consequently, they should be considered approximations and not the exact positions of the type localities.]

Non-type material. GHANA: Greater Accra Region, Accra Metropolis District, Legon, 23.VIII.1972 (*D. Leston*); NIGERIA: 16 km N. of Mokwa, 16.X.1976 (*C. Longhurst*).

Diagnosis. The following character combination separates *T. uelense* from the other species of the *T. decem* species group: relatively larger species (WL 0.98–1.06); propodeum armed with short triangular to elongate-triangular teeth (PSLI 16–18); petiolar node in profile around 1.1 times higher than long (LPeI 88–93); dorsum of mesosoma conspicuously longitudinally rugose with distinctive reticulate-punctate ground sculpture; strongly bicoloured with dark brown to black gaster contrasting with light brown to reddish brown remainder of body.

Worker measurements (N=6). HL 0.67–0.72 (0.70); HW 0.54–0.59 (0.57); SL 0.39–0.42 (0.41); EL 0.19–0.20 (0.20); PH 0.36–0.38 (0.37); PW 0.43–0.47 (0.45);

WL 0.98–1.06 (1.02); PSL 0.11–0.13 (0.10); PTL 0.27–0.29 (0.28); PTH 0.29–0.32 (0.31); PTW 0.21–0.23 (0.22); PPL 0.24–0.26 (0.25); PPH 0.28–0.34 (0.31); PPW 0.30–0.33 (0.31); CI 80–83 (81); SI 69–74 (72); OI 34–35 (35); DMI 43–44 (44); LMI 35–37 (36); PSLI 16–18 (17); PeNI 48–49 (49); LPeI 88–93 (90); DPeI 77–81 (79); PpNI 69–70 (70); LPpI 75–86 (80); DPpI 122–125 (124); PPI 141–145 (143).

Worker description. Head much longer than wide (CI 80–83); posterior head margin weakly concave. Anterior clypeal margin with distinct, but often shallow median impression. Frontal carinae strongly developed and noticeably raised forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and ventral scrobe margins; antennal scrobes very well developed, deep and with clearly defined margins, but ventral margin less strongly developed, median scrobal carina absent. Antennal scapes short, far from reaching posterior head margin (SI 69–74). Eyes relatively large (OI 34–35). Mesosomal outline in profile relatively flat, elongate and low (LMI 35–37), moderately to strongly marginate from lateral to dorsal mesosoma; promesonotal suture absent; metanotal groove present, distinct, but relatively shallow. Propodeum armed with short, triangular to elongate-triangular, and acute teeth (PSLI 16–18), propodeal lobes reduced, short, and well rounded, usually shorter than propodeal teeth. Tibiae and femorae strongly swollen. Petiolar node nodiform with moderately rounded antero- and posterodorsal margins, in profile around 1.1 times higher than long (LPeI 88–93), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height and equally angled, petiolar dorsum clearly convex; node in dorsal view around 1.2 to 1.3 times longer than wide (DPeI 77–81), in dorsal view pronotum between 2.0 and 2.1 times wider than petiolar node (PeNI 48–49). Postpetiole in profile globular, approximately 1.2 to 1.3 times higher than long (LPpI 75–86); in dorsal view between 1.2 and 1.3 times wider than long (DPpI 122–125), pronotum around 1.4 times wider than postpetiole (PpNI 69–70). Postpetiole in profile more or less of same volume as petiolar node, postpetiole in dorsal view around 1.4 times wider than petiolar node (PPI 141–145). Mandibles and clypeus unsculptured, smooth, and shining; cephalic dorsum between frontal carinae with fine irregularly longitudinally rugulose/rugose sculpture, rugulae/rugae often interrupted, meandering, or with cross-meshes, cephalic dorsum also punctulate to punctate throughout its length; scrobal area strongly reticulate-punctate; lateral head mainly reticulate-rugose with weak to moderately well developed punctate ground sculpture. Ground sculpture on head usually weak, except scrobal area (see above). Dorsum of mesosoma densely longitudinally rugose on top of strong punctate ground sculpture; lateral mesosoma longitudinally rugose and very conspicuously reticulate-punctate. Forecoxae unsculptured, smooth, and shining. Petiolar node and postpetiole superficially longitudinally rugulose or irregularly rugulose superimposed on conspicuous but relatively weak reticulate-punctate ground sculpture. Mesosoma and waist segments appearing matt. First gastral tergite unsculptured, smooth, and shiny. Pilosity and pubescence greatly reduced: head with few pairs of moderately long, standing hairs, anterior pronotum with one long pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one long pair; appressed pu-

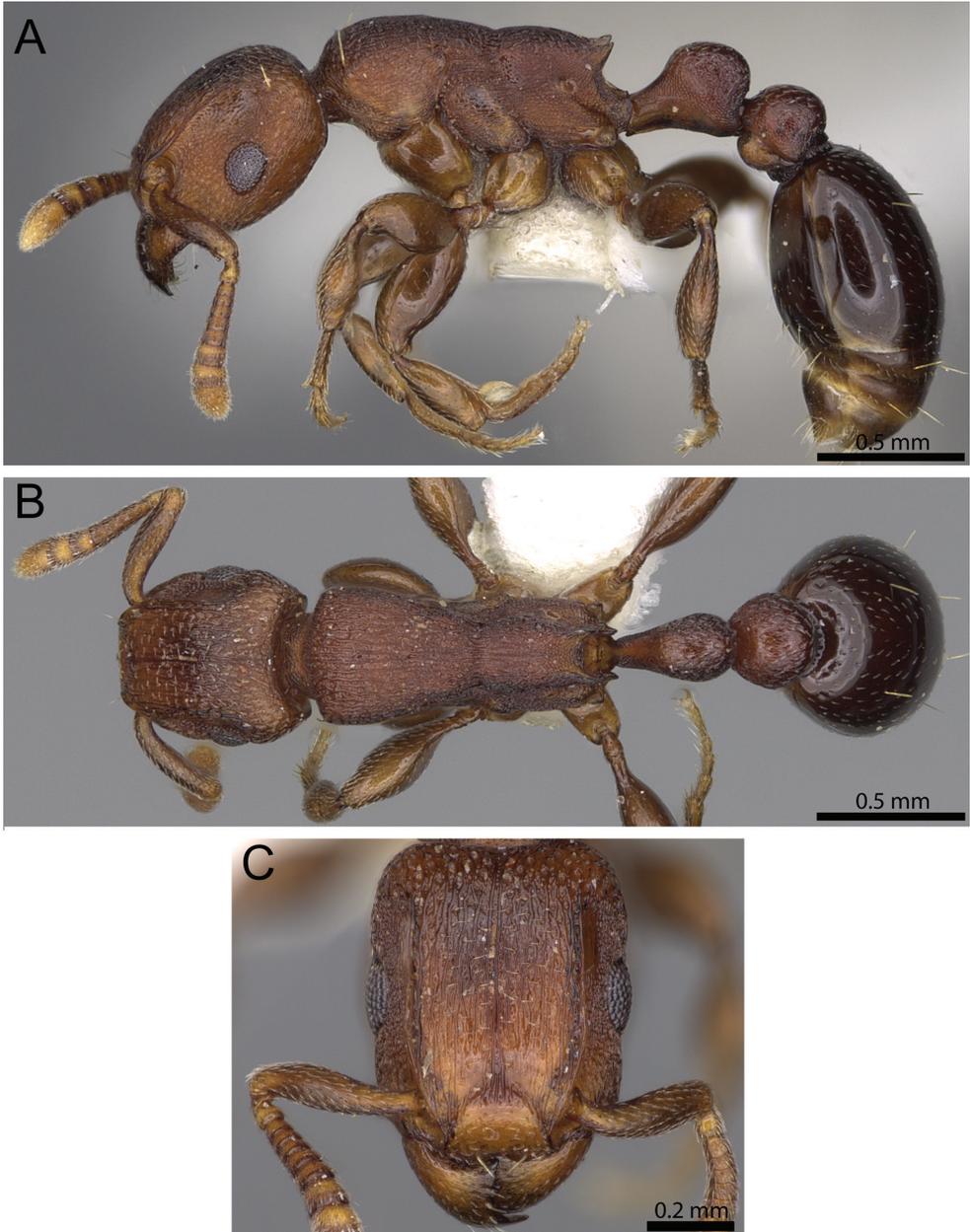


Figure 10. *T. uelense* non-type worker (CASENT0195580). **A** Body in profile **B** Body in dorsal view **C** Head in full-face view.

bescence present everywhere on body, but noticeable only on antennae, cephalic dorsum, legs, and first gastral tergite. Anterior edges of antennal scapes and dorsal (outer) surfaces of hind tibiae with appressed hairs. Body strongly bicoloured with dark brown to black gaster contrasting with light brown to reddish brown remainder.

Distribution and biology. So far, *T. uelense* is known from a few collections in savannah habitats throughout a relatively wide geographical range from West to Central Africa (Fig. 3). The known distribution spans Guinea through Ghana and Nigeria to the northeast of the D. R. Congo close to South Sudan and Uganda. Compared to most other Afrotropical *Tetramorium* species, there is a wealth of information about the natural history of *T. uelense* (Longhurst, 1979). Longhurst et al. (1979) provided important observation data about nests, foraging, recruitment, and predation on termites. *Tetramorium uelense* live in subterranean nests difficult to locate without observing foraging workers. At least in the area observed by Longhurst et al. (1979), the main prey of *T. uelense* consisted of various species of *Microtermes* Wasmann, and *T. uelense* exerted great predation pressure on these small termites. Scouting is performed by solitary workers that search the leaf litter, fallen grass stems or pieces of wood for prey. After locating termites the scouts return to the colony for recruitment of groups between 10 to 30 workers. These groups locate, immobilise, and retrieve the prey. For more details refer to Longhurst et al. (1979).

Discussion. *Tetramorium uelense* can be easily distinguished from the remainder of the *T. decem* species group. The presence of longitudinally rugose sculpture on the dorsum of the mesosoma separates *T. uelense* immediately from *T. decem*, *T. ultor*, and *T. venator*. In the latter three the mesosomal dorsum is completely unsculptured, smooth, and very shiny. The only other species with sculpture on the dorsum of the mesosoma, which could be confused with *T. uelense*, is *T. raptor*. Nevertheless, both are well separable in morphology and ecology. Most obviously, *T. uelense* is a larger species (WL 0.98–1.06) with distinct bicolouration while *T. raptor* (WL 0.88–0.93) is smaller and a uniform dark brown colour. In addition, *T. uelense* has longer and better developed propodeal teeth (PSLI 16–18) compared to *T. raptor* (PSLI 10–11), even though this might be difficult to see and may require measurements to confirm. Another, more visible character is the sculpture on the mesosomal dorsum, which is strongly longitudinally rugose with distinct punctate ground sculpture in *T. uelense* versus longitudinally rugulose with very little ground sculpture in *T. raptor*. Also, the lateral pronotum of the latter is mostly unsculptured, smooth, and shiny while in *T. uelense* the lateral pronotum is strongly rugose with conspicuous ground sculpture.

Variation. Despite the broad distribution range, we did not observe any significant intraspecific variation in *T. uelense*.

***Tetramorium ultor* Forel, 1913b, comb. r., stat. r. & stat. n.**

Figs 3, 4C, 7A, 7B, 11

Tetramorium (Decamorium) decem ultor Forel, 1913b: 217. [Combination in *Decamorium* by Wheeler 1922: 906; junior synonym of *Decamorium decem* by Bolton 1976: 298.]

Type material. Lectotype [designated here], pinned worker, ZIMBABWE, Shiloh, 19.73333 S, 28.55 E, 12.V.1913 (*G. Arnold*) (MHNG: CASENT0909197)

[examined]. **Paralectotypes**, seven pinned workers with same data as lectotype (BMNH: CASENT0901036; MHNG: CASENT0195688) [examined].

[Note: the GPS data of the type locality was not provided by the locality label or the original description. The data presented above is based on our own geo-referencing of the Shiloh locality located in Matabeleland North province. Consequently, it should be considered an approximation and not the exact position of the type locality.]

Non-type material. MOZAMBIQUE: Sofala Province, Gorongosa National Park, Limestone Gorge, 18°57'13"S, 34°10'37.6"E, 81 m, 15.V.2012 (*G.D. Alpert & E.O. Wilson*); Sofala Province, Gorongosa National Park, 5 km S Chitango, 18°59'28.8"S, 34°21'10"E, 10 m, secondary forest, 1.VI.2012 (*G.D. Alpert*); Sofala Province, Gorongosa National Park, Centrao Outpost (Piva-Joao), 18°30'20"S, 34°29'7"E, small forest along river, 11.VI.2012 (*D. Muala & T. Torcida*); Sofala Province, Gorongosa National Park, WP092, 18°56.1'3.1"S, 34°23'36.7"E, 51 m, open area, 26.VI.2012 (*G.D. Alpert*); KENYA: Kwale District, Shimba Hills, Longomagandi National Reserve, 4.23 S, 39.43 E, primary hardwood forest, 2.VI.2001 (*R.R. Snelling*); TANZANIA: Pwani, Rufiji District, Kichi Hills Forest Reserve, 8.23889 S, 38.65023 E, 499 m, primary forest, 5.–7.III.2008 (*P. Hawkes, Y. Mlacha, & F. Ninga*); ZAMBIA: Southern Province, 16.79533 S, 26.93833 E, 1330 m, Choma, Gwembe Lodge, miombo woodland, 3.XII.2005 (*B.L. Fisher*); ZIMBABWE: Balla-Balla, 20.45 S, 29.03 E, 1.IV.1945; Umtali, II.1917 (*G. Arnold*).

Diagnosis. *Tetramorium ultor* can be recognised by the following combination of characters: relatively smaller species (WL 0.85–0.96); very large eyes (OI 33–36); propodeum armed with short teeth (PSLI 10–13); petiolar node in profile around 1.1 to 1.2 times higher than long (LPeI 86–92); dorsum of promesonotum unsculptured, smooth, and very shiny; body of uniform light to chestnut brown, appendages often lighter.

Worker measurements (N=25). HL 0.62–0.70 (0.66); HW 0.48–0.58 (0.53); SL 0.35–0.42 (0.37); EL 0.16–0.20 (0.19); PH 0.29–0.33 (0.30); PW 0.37–0.45 (0.41); WL 0.85–0.96 (0.89); PSL 0.07–0.09 (0.08); PTL 0.22–0.25 (0.24); PTH 0.25–0.29 (0.27); PTW 0.19–0.22 (0.20); PPL 0.19–0.23 (0.21); PPH 0.25–0.30 (0.27); PPW 0.24–0.30 (0.27); CI 77–82 (80); SI 67–73 (70); OI 33–36 (35); DMI 44–48 (46); LMI 32–35 (34); PSLI 10–13 (12); PeNI 46–50 (48); LPeI 86–92 (88); DPeI 79–86 (84); PpNI 60–71 (67); LPpI 73–81 (78); DPpI 126–132 (130); PPI 130–145 (139).

Worker description. Head much longer than wide (CI 77–82); posterior head margin weakly concave. Anterior clypeal margin with distinct, but often shallow median impression. Frontal carinae strongly developed and noticeably raised forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and ventral scrobe margins; antennal scrobes very well developed, deep and with clearly defined margins all around, median scrobal carina absent. Antennal scapes short, not reaching posterior head margin (SI 67–73). Eyes very large (OI 33–36). Mesosomal outline in profile relatively flat, long and low (LMI 32–35), moderately marginate from lateral to dorsal mesosoma; promesonotal suture absent; metanotal groove present and distinct, but relatively shallow. Propodeum armed with short, tri-

angular, and mostly blunt teeth (PSLI 10–13), propodeal lobes short, triangular, and usually blunt, in profile usually longer and more voluminous than propodeal spines. Tibiae and femorae strongly swollen. Petiolar node nodiform with moderately rounded antero- and posterodorsal margins, in profile around 1.1 to 1.2 times higher than long (LPeI 86–92), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height and equally angled, petiolar dorsum weakly convex; node in dorsal view around 1.1 to 1.2 times longer than wide (DPeI 79–86), in dorsal view pronotum between 2.0 to 2.2 times wider than petiolar node (PeNI 46–50). Postpetiole in profile globular, approximately 1.2 to 1.4 times higher than long (LPpI 73–81); in dorsal view around 1.3 times wider than long (DPpI 126–132), pronotum approximately 1.4 to 1.5 times wider than postpetiole (PpNI 60–71). Postpetiole in profile appearing less voluminous than petiolar node, postpetiole in dorsal view between 1.3 to 1.5 times wider than petiolar node (PPI 130–145). Mandibles and clypeus usually fully unsculptured, smooth, and shining; cephalic dorsum between frontal carinae mostly unsculptured and shiny, median ruga present and distinct, cephalic dorsum also punctulate to punctate throughout its length, close to posterior head margin especially pronounced; scrobal area unsculptured, smooth, and very shiny; lateral head ventral of antennal scrobe mainly reticulate-rugose; ground sculpture on head usually weak to absent. Dorsum of mesosoma mostly unsculptured, smooth, and shiny with scattered punctures, rarely with few traces of rugulae; lateral mesosoma mostly unsculptured and shiny, posteriorly irregularly rugose and conspicuously reticulate-punctate. Petiolar node and postpetiole only weakly sculptured, laterally usually superficially rugulose and punctate on lower half and more unsculptured on upper half, node dorsally mostly smooth; postpetiole mostly unsculptured, smooth, and shiny with scattered punctures. First gastral tergite unsculptured, smooth, and shiny. Pilosity and pubescence greatly reduced: head with few pairs of moderately long, standing hairs, anterior pronotum with one long pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one long pair; appressed pubescence present everywhere on body, but noticeable only on antennae, cephalic dorsum, legs, and first gastral tergite. Anterior edges of antennal scapes and dorsal (outer) surfaces of hind tibiae with appressed hairs. Body uniformly brown, appendages often lighter.

Distribution and biology. *Tetramorium ultor* is widespread in eastern and southern Africa (Fig. 3). It is distributed from Kenya south to Mozambique, and also found in Zambia and Zimbabwe. Most localities are tropical dry forest habitats or miombo woodland. Also, *T. ultor* seems to be a ground-active species nesting in or under rotten logs and is likely termitophagous like the other group members.

Discussion. Since Bolton (1976) synonymised *T. ultor* under *T. decem*, almost all of the material of *T. ultor* examined here was identified and/or labelled as *T. decem* prior to this study. However, after careful examination of all the available material, we have come to the conclusion that *T. ultor* is distinctive enough to merit species status. *Tetramorium ultor* is smaller (WL 0.85–0.96), has shorter propodeal teeth (PSLI 10–13), a lower petiolar node, around 1.1 to 1.2 times higher than long (LPeI 86–92),

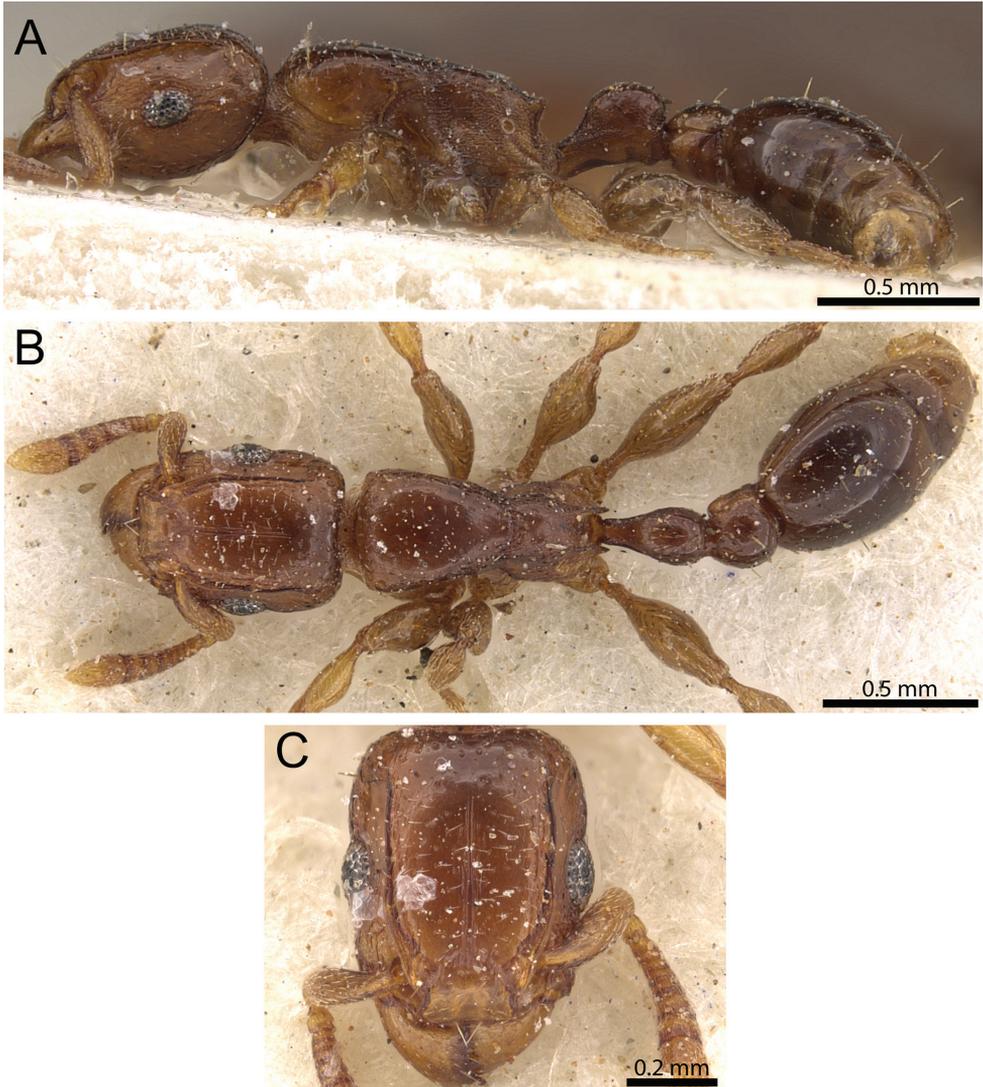


Figure 11. *T. ultor* paralectotype worker (CASENT0901036). **A** Body in profile **B** Body in dorsal view **C** Head in full-face view.

and is of uniform light brown to chestnut brown body colouration. By contrast, *T. decem* is larger (WL 1.02–1.16), has longer propodeal spines (PSLI 17–19), a higher petiolar node, in profile around 1.2 to 1.3 times higher than long (LPeI 77–82), and is conspicuously bicoloured. In addition, both species share most of their distribution range without any intermediate forms. Furthermore, *T. ultor* is unlikely to be confused with *T. raptor* and *T. uelense* since the latter two have a conspicuously rugose/rugulose promesonotum, which is completely unsculptured, smooth and shiny in *T. ultor*. The last species of the group, *T. venator*, is the one most similar to *T. ultor*, and

both species are allopatric. However, both species can be separated by eye size, colour, and a different habitat choice. *Tetramorium venator* has larger eyes (OI 37–40) and is of a much darker brown than *T. ultor*, which has smaller eyes (OI 33–36) and is of a lighter brown. In addition, the latter species is more arid-adapted, occurring in woodlands and dry forests while *T. venator* seems to be a forest specialist found in primary, secondary, or disturbed rainforests. We consider the above arguments as sufficient to justify the heterospecificity of both species. Further arguments are provided below in the description of *T. venator*.

Variation. Based on the available material, we did not observe any intraspecific variation in *T. ultor*.

***Tetramorium venator* Hita Garcia, sp. n.**

<http://zoobank.org/02C5E77F-FFD9-4204-843C-1E541B84972A>

http://species-id.net/wiki/Tetramorium_venator

Figs 3, 4D, 6B, 7C, 7D, 12

Type material. Holotype, pinned worker, KENYA, Western Kenya, Kakamega Forest, Bunyala Forest Fragment, 0.37889 N, 34.69917 E, 1448 m, disturbed primary forest, Kakamega 2008 survey, leaf litter, pitfall trap, Transect 35, position 10 m, 1.VIII.2008 (*G. Fischer*) (CASC: CASENT0195574). **Paratypes**, six pinned workers with same data as holotype (BMNH: CASENT0195625; CASC: CASENT0217165; BMNH: CASENT0195625; LACM: CASENT0195627; MCZ: CASENT0195624; NMK: CASENT0195626; ZFMK: CASENT0195623).

Non-type material. CAMEROON: Centre, Mbalmayo, 1.XI.1993 (*N. Stork*); Centre, Ottotomo, 24.IV.1986 (*A. Dejean*); Est, Abong Mbang, 28.VI.1988 (*A. Dejean*); Sud, Bondé Forest, N'kolo village, 27.5 km 155°SSE Elogbatindi, 3.22167 N, 10.24667 E, 40 m, rainforest, 12.IV.2000 (*B.L. Fisher*); Sud, Res. de Faune de Campo, Massif des Mamelles, 15.1 km 84°E Ébodjé, 2.59417 N, 9.9595 E, 180 m, rainforest, 4.IV.2000 (*B.L. Fisher*); Sud, Res. de Faune de Campo, 2.16 km 106°ESE Ébodjé, 2.56783 N, 9.84433 E, 10 m, littoral rainforest, 9.IV.2000 (*B.L. Fisher*); Sud, P. N. Campo, 43.3 km 108°ESE Campo, 2.2825 N, 10.20617 E, 290 m, rainforest, 7.IV.2000 (*B.L. Fisher*); Sud-Ouest, Bimbia Forest, 7.4 km 119°ESE Limbe, 3.98183 N, 9.2625 E, 40 m, 14.IV.2000 (*B.L. Fisher*); Sud-Ouest, Korup N. P., 6.9 km 317°NW Mundemba, 5.016 N, 8.864 E, 110 m, rainforest, 19.IV.2000 (*B.L. Fisher*); CENTRAL AFRICAN REPUBLIC: Prefecture Sangha-Mbaéré, Parc National Dzanga-Ndoki, Mabéa Bai, 21.4 km 53°NE Bayanga, 3.03333 N, 16.41 E, 510 m, rainforest, 1.–7.V.2001 (*B.L. Fisher*); DEMOCRATIC REPUBLIC OF CONGO: Epulu, 750 m, 1.38333 N, 28.58333 E, rainforest, 1.XI.1995 (*S.D. Torti*); Kikwit, Kinzambi, 27.III.1984 (*A. Dejean*); 44 miles E. of Kileba, 1110 m, 16.I.1958 (*E.S. Ross & R.E. Leech*); GABON: La Makandé Forêt des Abeilles, 1.I.–1.II.1999 (*S. Lewis*); Ogooué-Ivindo, Makokou, C.N.R.S., 10.VII.1974 (*W. Gotwald*); Ogooue-Maritime, Réserve des Monts Doudou, 24.3km 307°NW Doussala, 2.2225 S, 10.40583 E, 370 m, coastal lowland rainforest,

5.–12.III.2000 (*S. van Noort*); Ogooue-Maritime, Aire d'Exploit. Rationnelle de Faune des Monts Doudou, 24.3 km 307°NW Doussala, 2.22639 S, 10.40972 E, 375 m, rainforest, 6.III.2000 (*B.L. Fisher*); Ogooue-Maritime, Reserve de la Moukalaba-Dougoua, 12.2 km 305°NW Doussala, 2.28333 S, 10.49717 E, 110 m, coastal lowland rainforest, sited within forest, 24.II.–3.III.2000 (*S. van Noort*); Ogooue-Maritime, Reserve de Faune de la Moukalaba-Dougoua, 10.8 km 214°SW Doussala, 2.42267 S, 10.54533 E, 110 m, rainforest, 29.II.2000 (*B.L. Fisher*); Ogooue-Maritime, Reserve de Faune de la Moukalaba-Dougoua, 12.2 km 305°NW Doussala, 2.31667 N, 10.53333 E, 110 m, rainforest, 1.III.2000 (*B.L. Fisher*); Woleu-Ntem, 31.3 km 108°ESE Minvoul, 2.08 N, 12.40667 E, 600 m, rainforest, 7.–15.II.1998 (*B.L. Fisher*); GHANA: Akwapim, Tafo, 19.I.1970 (*B. Bolton*); Ashanti, Poano, cocoa, 9.IX.1992 (*R. Belshaw*); Atewa Forest Reserve, near Kibi, primary forest, 24.III.1992 (*R. Belshaw*); Eastern, Kade, 1.I.1992 (*R. Belshaw*); Enchi, 17.V.1969 (*D. Leston*); Esunkawkaw Forest Reserve, primary forest, 27.X.1992 (*R. Belshaw*); Nkawanda near Nkawkaw, secondary forest, 12.XII.1991 (*R. Belshaw*); Portrasi, 1.III.1992 (*R. Belshaw*); KENYA: Western Kenya, Kakamega Forest, Bunyala Forest Fragment, 0.37889 N, 34.69917 E, 1448 m, disturbed primary forest, 1.VIII.2008 (*G. Fischer*); LIBERIA: Monrovia, 5.VII.1957 (*E.S. Ross & R.E. Leech*); TANZANIA: Kigoma Region, Gombe Stream National Park, 4.7 S, 29.616667 E, 915–1012 m, 29.XII.2009–12.I.2010 (*R. O'Malley*); UGANDA: Semuliki NP, 00.83556, 30.15542 ± 200 m, 676 m, rainforest, 30.–31.VII.2012 (*B.L. Fisher et al.*); Semuliki NP, 00.84483, 30.15052 ± 200 m, 680 m, rainforest, 2.VIII.2012 (*B.L. Fisher et al.*).

Diagnosis. *Tetramorium venator* can be recognised by the following combination of characters: relatively smaller species (WL 0.87–0.98); very large eyes, largest in the group (OI 37–40); propodeum armed with very short, triangular, and moderately acute (PSLI 9–12); petiolar node in profile between 1.0 to 1.2 times higher than long (LPeI 90–100); dorsum of promesonotum unsculptured, smooth, and very shiny; head, mesosoma, waist segments, and gaster uniformly very dark brown to black, appendages of lighter brown.

Worker measurements (N=25). HL 0.64–0.71 (0.67); HW 0.51–0.59 (0.54); SL 0.38–0.43 (0.40); EL 0.19–0.22 (0.21); PH 0.30–0.36 (0.32); PW 0.39–0.45 (0.41); WL 0.87–0.98 (0.92); PSL 0.06–0.09 (0.07); PTL 0.23–0.26 (0.25); PTH 0.25–0.29 (0.26); PTW 0.18–0.22 (0.20); PPL 0.21–0.25 (0.22); PPH 0.25–0.30 (0.26); PPW 0.25–0.30 (0.26); CI 79–83 (81); SI 70–75 (74); OI 37–40 (38); DMI 43–46 (44); LMI 33–37 (35); PSLI 9–12 (10); PeNI 45–51 (48); LPeI 90–100 (93); DPeI 76–85 (80); PpNI 63–67 (65); LPpI 80–86 (84); DPpI 115–124 (119); PPI 130–144 (135).

Worker description. Head much longer than wide (CI 79–83); posterior head margin weakly concave. Anterior clypeal margin with distinct, but often shallow median impression. Frontal carinae strongly developed and noticeably raised forming dorsal margin of very well-developed antennal scrobes, curving down ventrally and anteriorly halfway between posterior eye margin and posterior head margin and forming posterior and ventral scrobe margins; antennal scrobes very well developed, deep and with clearly defined margins all around, median scrobal carina absent. Antennal scapes short, not reaching posterior head margin (SI 70–75). Eyes very large (37–40).

Mesosomal outline in profile relatively flat, long and low (LMI 33–37), moderately marginate from lateral to dorsal mesosoma; promesonotal suture absent; metanotal groove present and distinct, but relatively shallow. Propodeum armed with very short, triangular, and moderately acute teeth (PSLI 9–12), propodeal lobes short, triangular to rounded, and usually blunt, in profile more or less of same length as propodeal teeth and appearing more voluminous than propodeal spines. Tibiae and femorae strongly swollen. Petiolar node nodiform with moderately rounded antero- and posterodorsal margins, in profile between 1.0 to 1.2 times higher than long (LPeI 90–100), anterior and posterior faces approximately parallel, anterodorsal and posterodorsal margins situated at about same height and equally angled, petiolar dorsum usually conspicuously convex, sometimes only weakly so; node in dorsal view around 1.2 to 1.3 times longer than wide (DPeI 76–85), in dorsal view pronotum between 2.0 to 2.2 times wider than petiolar node (PeNI 45–51). Postpetiole in profile globular, approximately 1.2 times higher than long (LPpI 80–86); in dorsal view around 1.2 times wider than long (DPpI 115–124), pronotum approximately 1.5 to 1.6 times wider than postpetiole (PpNI 63–67). Postpetiole in profile appearing less voluminous than petiolar node, postpetiole in dorsal view between 1.3 to 1.5 times wider than petiolar node (PPI 130–144). Mandibles and clypeus usually fully unsculptured, smooth, and shining; cephalic dorsum between frontal carinae mostly unsculptured and shiny, median ruga present and distinct, cephalic dorsum also punctulate to punctate across its length, close to posterior head margin especially pronounced; scrobal area unsculptured, smooth and very shiny; lateral head ventral of antennal scrobe mainly reticulate-rugose; ground sculpture on head usually weak to absent. Dorsum of mesosoma mostly unsculptured, smooth and shiny with scattered punctures, rarely with few traces of rugulae; lateral mesosoma mostly unsculptured and shiny, posteriorly irregularly rugose and conspicuously reticulate-punctate. Petiolar node and postpetiole only weakly sculptured, laterally usually superficially rugulose and punctate on lower half and more unsculptured on upper half, node dorsally mostly smooth; postpetiole mostly unsculptured, smooth and shiny with scattered punctures. First gastral tergite unsculptured, smooth, and shiny. Pilosity and pubescence greatly reduced: head with few pairs of moderately long, standing hairs, anterior pronotum with one long pair, waist segments sometimes with one long pair each, and sometimes first gastral tergite with one long pair; appressed pubescence present everywhere on body, but noticeable only on antennae, cephalic dorsum, legs, and first gastral tergite. Anterior edges of antennal scapes and dorsal (outer) surfaces of hind tibiae with appressed hairs. Head, mesosoma, waist segments, and gaster uniformly very dark brown to black, appendages of lighter brown.

Etymology. The name of the new species is Latin and means “hunter” referring to the predatory lifestyle of *T. venator*. The species epithet is a nominative noun, and thus invariant.

Distribution and biology. *Tetramorium venator* is the most widespread and abundant species of the group. It is found throughout much of the equatorial forest belt from Liberia in the west to Kenya in the east (Fig. 3). Even though there was no material from Benin, Togo, Nigeria, Equatorial Guinea or South Sudan available for this study, we

expect that *T. venator* will be found in most or all of these countries. Based on the available data, this species lives in the leaf litter stratum of primary, secondary, or disturbed rainforests. Additionally, *T. venator* seems to be found at lower elevations in West and Central Africa, but also occurs at mid elevations further east in the eastern D.R. Congo, Tanzania, and Kenya, where it reaches its highest known elevation at the type locality at 1448 m. Based on unpublished stable isotope data from the type series, *T. venator* is a predatory species, and we assume that it feeds on termites. This is supported by some series from Cameroon that were collected while foraging in the nests of *Cubitermes* Wasmann.

Discussion. Despite being common and collected fairly often prior to this study, most of the material of *T. venator* was identified and labelled as *T. decem*. Indeed, more than 90% of all the material listed as the latter species at the beginning of our revision turned out to be *T. venator*. Nevertheless, our revision shows that they are clearly not conspecific. *Tetramorium venator* is smaller in size (WL 0.87–0.98), has larger eyes (OI 37–40), shorter propodeal teeth (PSLI 9–12), a lower petiolar node (LPeI 90–100), and has a uniform body colouration. By contrast, *T. decem* is larger (WL 1.02–1.16), has smaller eyes (OI 32–34), longer propodeal spines (PSLI 17–19), a higher petiolar node (LPeI 77–82), and is distinctly bicoloured. Also, *T. venator* is a rainforest species while *T. decem* lives in savannah or woodland.

The abovementioned very large eyes of *T. venator* separate it also from *T. ultor*, which has smaller eyes (OI 33–36). In addition, *T. ultor* is also of a much lighter colour, usually light brown to chestnut brown, and prefers dry forest or woodland habitats. It should be noted, however, that *T. ultor* and *T. venator* are morphologically very close to each other and differ significantly only in eye size, colour and habitat preference. They could represent different ecotypes of the same species, one adapted to more shaded and humid forest versus one specialised to more arid savannah, woodland, and dry forest. Nevertheless, if this was true, then we would see some intermediate forms in transitional habitats, and there are none at present. As a matter of fact, *T. venator* is also found in secondary and disturbed rainforests. The type series was collected in a highly disturbed rainforest fragment in Kenya and the material from Gombe in Tanzania is from a rainforest-woodland mosaic. Both species are also separated by the Great Rift Valley, which separates different faunistic sub-regions of the Afrotropical region. We consider *T. venator* as a faunal element of the Guineo-Congolian forest zone, while we believe *T. ultor* is a species of the arid corridor running from East to Southern Africa. Based on the available material and African biogeography in general, we conclude that our two species hypothesis is more likely.

Furthermore, *T. venator* cannot be misidentified with either *T. uelense* or *T. raptor* since both possess strongly developed rugulose/rugose sculpture on the promesonotal dorsum that is absent in *T. venator*. At present, *T. venator* overlaps in its distribution with *T. uelense* and *T. raptor* in West and Central Africa. We think it might also overlap with *T. decem* and *T. ultor* in East Africa, even though it currently seems as if they are widely separated geographically. However, since the sampling is very patchy, especially in East Africa, much more *T. decem* and *T. ultor* material is likely to be collected with further inventories, and these two species will be found in close proximity to *T. venator*. Never-

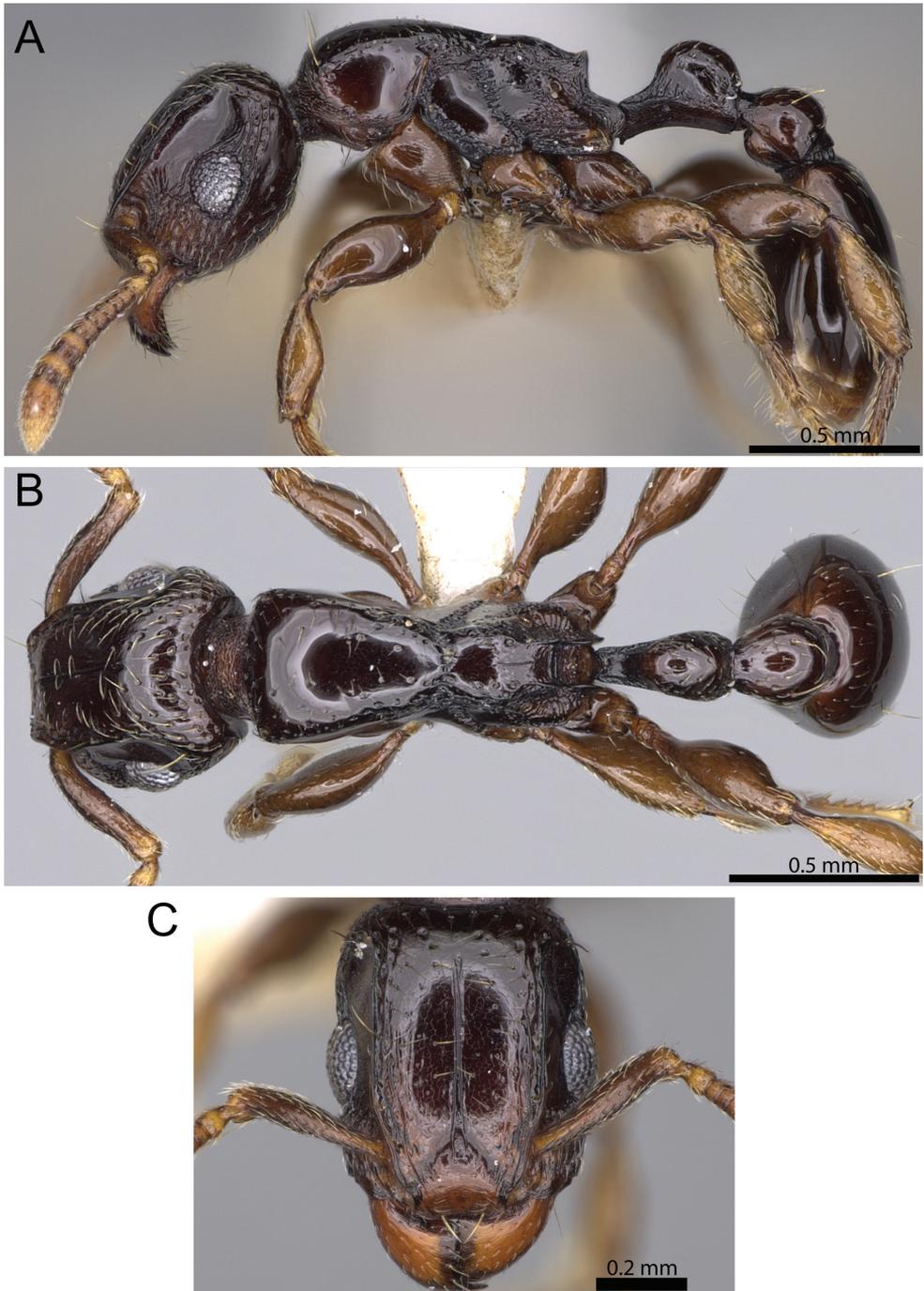


Figure 12. *T. venator* holotype worker (CASENT0195574). **A** Body in profile **B** Body in dorsal view **C** Head in full-face view.

theless, the latter species is restricted to more humid forest habitats, whereas *T. decem* and *T. ultor* clearly prefer more arid savannah, grassland, woodland and tropical dry forest.

Variation. Intriguingly, even though *T. venator* is very broadly distributed in Equatorial Africa, there seems to be no significant intraspecific variation.

Acknowledgments

First we thank Michele Esposito from CAS for her help with image processing and databasing. We are also indebted to Dr. Georg Fischer from CAS for his general help with Afrotropical ants and the good time in the field with FHG. He also collected and processed a good number of specimens from East Africa used in this study. We want to thank Dr. Gary D. Alpert from MCZ for providing very important material from Mozambique. In addition, we want to express our gratitude to Marek Borowiec, Barry Bolton, and one anonymous reviewer for suggestions, comments, and critique that have improved the manuscript. Furthermore, we are thankful to the following curators and/or curatorial staff, who either loaned important material or welcomed FHG to their collections: Mrs Suzanne Ryder, Dr. Gavin Broad, Mrs Natalie Dale-Skey Papilloud from BMNH; Dr. Stefan Cover and Dr. Gary D. Alpert from MCZ; Dr. Giulio Cuccodoro from MHNG; Mrs Isabelle Zürcher-Pfander from NHMB; Dr. Brian Brown and Mrs Giar-Ann Kung from LACM; and Dr. Eliane De Coninck from RMCA. This study was partially supported by the National Science Foundation under Grant No. DEB-0842395 granted to BLF and two Ernst Mayr Travel Grants from the MCZ granted to FHG to visit the collections in BMNH and MCZ.

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Morphological and molecular affinities of two East Asian species of *Stenhelia* (Crustacea, Copepoda, Harpacticoida)

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Abstract

Definition of monophyletic supraspecific units in the harpacticoid subfamily Stenheliinae Brady, 1880 has been considered problematic and hindered by the lack of molecular or morphology based phylogenies, as well as by incomplete original descriptions of many species. Presence of a modified seta on the fifth leg endopod has been suggested recently as a synapomorphy of eight species comprising the redefined genus *Stenhelia* Boeck, 1865, although its presence was not known in *S. pubescens* Chislenko, 1978. We re-describe this species in detail here, based on our freshly collected topotypes from the Russian Far East. The other species redescribed in this paper was collected from the southern coast of South Korea and identified as the Chinese *S. taiae* Mu & Huys, 2002, which represents its second record ever and the first one in Korea. A fragment of the mtCOI gene was successfully PCR-amplified from two specimens of each species, which represents the first molecular data for this genus, and from additional 19 specimens belonging to six different species of other stenheliins from Korea and Russia. Reconstructed phylogenies confirm previously postulated monophyly of *Stenhelia* and polyphyly of the closely related genus *Delavalia* Brady, 1869. Average pairwise maximum likelihood distances between *S. pubescens* and *S. taiae* are only slightly above 10%, suggesting a very close relationship despite numerous newly discovered micro-morphological differences and despite macro-morphological similarities being probable plesiomorphies.

Keywords

Miraciidae, Stenheliinae, marine, systematics, phylogeny, DNA barcoding

Introduction

The subfamily Stenheliinae Brady, 1880 is currently recognised as one of three well-defined suprageneric groups within the second largest harpacticoid family Miraciidae Dana, 1846, beside the nominotypical subfamily and Diosaccinae Sars, 1906 (see Willen 2000; Boxshall and Halsey 2004; Wells 2007; Huys and Mu 2008). Stenheliins are common inhabitants of the marine benthos, and can be found from the deep sea (Willen 2003) to shallow brackish waters (Dussart and Defaye 2001). Although there is some disagreement about the exact number of morphological synapomorphies defining this subfamily (Willen 2000, 2002; Huys and Mu 2008), these six are undisputed for adults: laterally displaced genital apertures in females; triangular and usually bifid rostrum, with dorsal pair of sensilla inserted in deep anterior recesses; elongated basis and endopod of mandibula (often also with one extremely long and strong seta); maxilliped with only three syncoxal setae, closely positioned to one another, and setation of the ancestral second endopodal segment lost; female fifth leg with laterally directed exopod; and some form of sexual dimorphism in the second leg (although probably secondarily lost in several species). Some additional synapomorphies are postulated for their naupliar morphology (Dahms and Bresciani 1993, Dahms et al. 2005) but they need to be verified in a broader taxon sampling (Huys and Mu 2008). Ninety-three valid stenheliin species (Wells 2007; Walter and Boxshall 2014; Karanovic and Kim 2014) are currently classified into 12 genera: *Anisostenhelia* Mu & Huys, 2002 (monospecific); *Beatricella* T. Scott, 1905 (monospecific); *Cladorostrata* Tai & Song, 1979 (two species); *Delavalia* Brady, 1869 (53 species and subspecies); *Itostenhelia* Karanovic & Kim, 2014 (two species); *Melima* Por, 1964 (six species); *Muohuysia* Ozdikmen, 2009 (monospecific); *Onychostenhelia* Itô, 1979 (two species); *Pseudostenhelia* Wells, 1967 (four species); *Stenhelia* Boeck, 1865 (eight species); *Wellstenhelia* Karanovic & Kim 2014 (eight species), and *Willenstenhelia* Karanovic & Kim, 2014 (five species).

The most speciose and morphologically most diverse genus *Delavalia* is also taxonomically most problematic, and expectedly postulated to be either paraphyletic (Willen 2002) or polyphyletic (Mu and Huys 2002). Several groups of species were recognized in this genus by Willen (2003) and Huys and Mu (2008), mostly based on intuitive methods and without phylogenetic or nomenclatural consideration. Karanovic and Kim (2014) demonstrated the polyphyletic nature of *Delavalia* using molecular phylogenies and erected three new genera for nine new species and six previously described members of *Delavalia*, each supported by molecular data and a number of morphological synapomorphies. The latter authors used two *Stenhelia* species as outgroups in their molecular analyses, which are the subject of this paper.

The genus *Stenhelia* was redefined recently by Mu and Huys (2002) and restricted to a core group of species formerly allocated to the subgenus *Stenhelia* (*Stenhelia*). In addition to the type species, *S. gibba* Boeck, 1865, the genus currently contains the following seven species: *S. curviseta* Lang, 1936; *S. divergens* Nicholls, 1939; *S. peniculata* Lang, 1965; *S. proxima* Sars, 1906; *S. pubescens* Chislenko, 1978; *S. sheni* Mu & Huys, 2002; and *S. taiiae* Mu & Huys, 2002. Mu and Huys (2002) suggested the presence

of a modified seta on the fifth leg endopod as a generic synapomorphy, although its presence was not known in *S. pubescens*. This prompted us to redescribe this species in detail here, based on our freshly collected topotypes from the Russian Far East (Posyet Bay near Vladivostok). Another species of *Stenhelia* was collected from the southern coast of South Korea and identified as *S. taiiae*, originally described from China, which represents its second record ever and the first one in Korea. Beside detailed redescrptions of these two species, we also provide their mtCOI sequences, which represent the first molecular data for this genus. One of the aims was to test the generic monophyly reconstructing molecular phylogenies in a larger group of stenheliin copepods. We also aimed to test if the two *Stenhelia* species are closely related, as suggested by Mu and Huys (2002) based on the armature of the third leg endopod and the shape of the first leg endopod, because these seem to be in a plesiomorphic state in the two species when compared with other congeners.

Employing molecular techniques in addition to traditional morphological ones was one of the priorities of this study to aid in species delineation and reconstruction of their phylogenetic relationships. Recently, DNA-based species identification methods, referred to as “DNA barcoding”, have been widely employed to estimate levels of species diversity, with the 5’ end of the mitochondrial cytochrome C oxidase subunit 1 gene (mtCOI) proposed as the “barcode” for all animal species (Hebert et al. 2003). The advantage of the mtCOI gene is that it often shows low levels of genetic variation within species, but high levels of divergence between species; for the most common divergence values in a variety of crustacean taxa see Lefébure et al. (2006). In recent years several studies on copepods showed that combining molecular and morphological methods can help answer questions related to cryptic speciation (Bláha et al. 2010; Sakaguchi and Ueda 2010; Karanovic and Krajicek 2012a, Hamrova et al. 2012), invasions of new habitats and colonisation pathways (Lee et al. 2003, 2007; Winkler et al. 2008; Karanovic and Cooper 2011a, 2012), anthropogenic translocation (Karanovic and Krajicek 2012a), short range endemism and allopatry (Karanovic and Cooper 2011a), and definition of supraspecific taxa in conservative genera or families (Huys et al. 2006, 2007, 2009, 2012; Wyngaard et al. 2010; Karanovic and Cooper 2011b, Karanovic and Krajicek 2012b, Karanovic and Kim 2014). However, some studies showed that currently prevailing morphological methods of identifying copepod species are inadequate, and suggested the use of alternative microstructures, such as pores and sensilla pattern on somites (Alekseev et al. 2006; Karanovic and Krajicek 2012a; Karanovic and Cho 2012; Karanovic and Kim 2014; Karanovic and Lee 2012; Karanovic et al. 2012, 2013), an approach also tested in this study.

Material and methods

All Korean samples for this study were taken at seventeen stations in Gwangyang Bay, on the South Coast of South Korea, on four occasions: 18 February 2012, 30 July 2012, 14 October 2012, and 18 November 2012 (see Karanovic and Kim 2014).

Depth ranged from four to 11 metres and environmental conditions changed greatly with seasons; those measured on 18 January 2006 are presented in Table 1. We found no correlation between environmental data and distribution of stenheliins. A handheld multiparameter water quality meter YSI556 (YSI Environmental, Yellow Springs, USA) was used for all measurements, except for chlorophyll *a*, which was measured by manual filtering with different size filters, and temperature, which was measured with a mercury fill glass thermometer. Coordinates were taken with a Garmin GPS, model Oregon 300. Granular analysis of the sediment was conducted manually, following the methods and classification of Folk (1974). Sediment samples were primarily collected with a van Veen grab sampler (surface area: 0.1 m²) from the Hansan research vessel. Subsamples were then collected by acrylic corers (surface area: 10 cm²) for quantitative analysis, and surface sediments were collected by a small shovel for qualitative analysis. Each sediment sample was fixed in 99.9% ethanol. Animals in the sediments were extracted by Ludox method (Burgess 2001) and preserved in 99.9% ethanol for morphological or molecular studies. Specimens from Posyet Bay (Minonosok inlet) in Russia were collected with hand-nets (100 µm mesh size) using Scuba-diving from a sandy bottom and between four and seven metres of depth, and also fixed in 99.9% ethanol. Locality data and number of specimens are given in the Material examined section for each species below. All material is deposited at the National Institute of Biological Resources (NIBR), Incheon, South Korea.

Specimens were dissected and mounted on microscope slides in Faure's medium (see Stock and von Vaupel Klein 1996), and dissected appendages were then covered by a coverslip. For the urosome or the entire animal, two human hairs were mounted between the slide and coverslip, so the parts would not be compressed. All line drawings were prepared using a drawing tube attached to a Leica MB2500 phase-interference compound microscope, equipped with N-PLAN (5×, 10×, 20×, 40× and 63× dry) or PL FLUOTAR (100× oil) objectives. Specimens that were not drawn were examined in propylene glycol and, after examination, were again preserved in 99.9% ethanol. Specimens for scanning electron micrography (SEM) were dehydrated in progressive ethanol concentrations, transferred into pure isoamyl-acetate, critical-point dried, mounted on stubs, coated in gold, and observed under a Hitachi S-4700 microscope on the in-lens detector, with an accelerating voltage of 10 kV and working distances between 12.3 and 13.4 mm; micrographs were taken with a digital camera.

Morphological terminology follows Huys and Boxshall (1991), except for the numbering of the setae of the caudal rami and small differences in the spelling of some appendages (antennula, mandibula, maxillula instead of antennule, mandible, maxillule), as an attempt to standardise the terminology for homologous appendages in different crustacean groups. Sensilla and pores on all somites (body segments) were examined in detail, but are not numbered or marked otherwise on the figures. Only the first presented species is described in full, while the subsequent description is shortened by making it comparative.

Specimens for molecular analysis were examined without dissection under a compound microscope (objective 63× dry) in propylene glycol, using a cavity well slide

Table 1. Environmental conditions at 17 sampling stations in Gwangyang Bay, recorded on 18 January 2006. Water temperature was measured on the surface. Granular analysis was conducted manually according to the protocol described by Folk (1974). Abbreviations: WT, water temperature; ST, sediment temperature; Sal., salinity; DO, dissolved oxygen; Cond., conductivity.

Station	Temperature (C)		pH	Sal. (ppt)	DO (mg/L)	Chlorophyll a		Cond. (mS/cm)	Granular analysis			Coordinates
	WT	ST				total	nano		gravel	sand	mud	
St.01	5.9	7.0	8.1	33.3	11.5	4.6	2.2	32.8	0.0%	9.8%	90.2%	34.913194°N, 127.600917°E
St.02	6.3	7.1	8.1	33.3	11.0	4.5	0.6	33.1	0.0%	46.1%	53.9%	34.881861°N, 127.635083°E
St.03	5.1	7.0	7.9	33.4	12.5	5.2	2.9	32.8	1.9%	37.0%	63.0%	34.884417°N, 127.664028°E
St.04	5.1	7.8	8.2	31.8	12.0	3.1	1.5	30.8	0.1%	29.6%	70.4%	34.910722°N, 127.696806°E
St.05	6.0	7.3	7.3	33.4	10.8	8.9	8.9	32.9	0.0%	19.7%	80.3%	34.852500°N, 127.684722°E
St.06	6.3	7.2	8.1	33.3	12.0	4.1	2.0	33.1	0.0%	13.3%	86.7%	34.860861°N, 127.733417°E
St.07	6.4	8.3	8.2	33.4	12.3	6.7	1.4	33.3	0.0%	13.7%	86.3%	34.897056°N, 127.757722°E
St.08	6.8	8.8	8.2	32.2	10.8	3.9	0.3	32.6	0.0%	16.6%	83.4%	34.865417°N, 127.767222°E
St.09	5.9	7.3	7.5	27.1	12.9	-	-	27.2	0.0%	25.4%	74.6%	34.951389°N, 127.734361°E
St.10	5.9	8.1	8.2	29.5	12.8	3.7	0.9	29.4	0.1%	55.1%	44.9%	34.920944°N, 127.785528°E
St.11	7.7	8.1	7.9	33.4	10.1	0.5	0.4	34.4	0.0%	31.0%	69.0%	34.924333°N, 127.852333°E
St.12	5.8	8.3	8.2	30.7	11.5	3.8	0.4	30.4	0.0%	67.0%	33.0%	34.890139°N, 127.795111°E
St.13	6.6	9.2	8.1	33.2	11.5	5.6	1.5	33.3	0.4%	73.3%	26.7%	34.852750°N, 127.791000°E
St.14	6.6	8.1	8.2	33.3	10.9	5.0	3.8	33.3	0.0%	46.6%	53.4%	34.824222°N, 127.787750°E
St.15	6.9	7.7	8.2	33.6	10.8	3.2	1.1	33.9	0.3%	60.5%	39.5%	34.797194°N, 127.786444°E
St.16	6.7	7.5	8.2	33.8	10.9	6.6	3.5	34.0	2.5%	33.7%	66.3%	34.768889°N, 127.783806°E
St.17	6.2	7.7	8.2	33.8	10.5	4.4	1.6	33.5	0.0%	37.0%	63.0%	34.743444°N, 127.778972°E

with a central depression. After examination they were returned to 99.9% ethanol. Before amplification whole specimens were transferred into distilled water for two hours for washing (to remove ethanol), and then minced with a small glass stick. DNA was extracted from whole specimens, except in one case when only one antennula was available, using the LaboPassTM extraction kit (COSMO Co. Ltd., Korea) and following the manufacturer's protocols for fresh tissue, except that samples were incubated in the Proteinase K solution overnight, step five was skipped, and 60 instead of 200 μ l of Buffer AE was added in the final step, to increase the density of DNA. Mitochondrial cytochrome oxidase subunit I (mtCOI) gene was amplified through polymerase chain reaction (PCR) using PCR premix (BiONEER Co.) in TaKaRa PCR thermal cycler (Takara Bio Inc., Otsu, Shiga, Japan). The amplification primers used were the 'universal' primers LCO1490 and HCO2198 (Folmer et al. 1994). The amplification protocol was: initial denaturation 94 °C for 300 s, 40 cycles of denaturation 94 °C for 30 s, annealing at 42 °C for 120 s, extension at 72 °C for 60 s; final extension at 72 °C for 600 s, and final product was stored at 4 °C. PCR results were checked by electrophoresis of the amplification products on 1% agarose gel with ethidium bromide. PCR products were purified with a LaboPassTM PCR purification kit and sequenced in both directions using a 3730xl DNA analyzer (Macrogen, Korea). For this study, DNA was extracted and the COI fragment successfully PCR amplified from 23 stenheliin specimens (Table 2).

Table 2. List of copepod specimens for which mtCOI fragment was successfully amplified.

Code	Species	Country	Station	Date	Bases	GenBank
0330	<i>Itostenhelia golikovi</i>	Russia	Posyet Bay	06 May 2012	448	KF524863
0433	<i>Itostenhelia golikovi</i>	Russia	Posyet Bay	06 May 2012	515	KF524864
0631	<i>Itostenhelia golikovi</i>	Russia	Posyet Bay	06 May 2012	514	KF524865
0734	<i>Itostenhelia golikovi</i>	Russia	Posyet Bay	06 May 2012	503	KF524866
0832	<i>Itostenhelia golikovi</i>	Russia	Posyet Bay	06 May 2012	493	KF524867
0176	<i>Itostenhelia polyhymnia</i>	Korea	10	30 Jul 2012	660	KF524868
0273	<i>Itostenhelia polyhymnia</i>	Korea	10	30 Jul 2012	664	KF524869
0271	<i>Itostenhelia polyhymnia</i> L-form	Korea	10	30 Jul 2012	278	KF524883
8417	<i>Schizopera leptafurca</i>	Australia	YYAC0016A	20 Mar 2010	517	JQ390578
0152	<i>Stenhelia pubescens</i>	Russia	Posyet Bay	06 May 2012	659	KF524870
0254	<i>Stenhelia pubescens</i>	Russia	Posyet Bay	06 May 2012	647	KF524871
0163	<i>Stenhelia taiae</i>	Korea	16	18 Nov 2012	558	KF524884
0167	<i>Stenhelia taiae</i>	Korea	16	18 Nov 2012	662	KF524885
0122	<i>Wellstenhelia calliope</i>	Korea	5	30 Jul 2012	576	KF524872
0187	<i>Wellstenhelia clio</i>	Korea	10	30 Jul 2012	519	KF524873
0113	<i>Wellstenhelia qingdaoensis</i>	Korea	15	18 Nov 2012	518	KF524874
0143	<i>Willenstenhelia thalia</i>	Korea	10	30 Jul 2012	657	KF524875
0146	<i>Willenstenhelia thalia</i>	Korea	10	18 Nov 2012	664	KF524878
0241	<i>Willenstenhelia thalia</i>	Korea	10	30 Jul 2012	524	KF524876
0245	<i>Willenstenhelia thalia</i>	Korea	10	18 Nov 2012	662	KF524879
0342	<i>Willenstenhelia thalia</i>	Korea	10	30 Jul 2012	330	KF524877
0348	<i>Willenstenhelia thalia</i>	Korea	10	18 Nov 2012	660	KF524880
0444	<i>Willenstenhelia thalia</i>	Korea	10	18 Nov 2012	667	KF524881
0547	<i>Willenstenhelia thalia</i>	Korea	10	18 Nov 2012	661	KF524882

Obtained sequences were checked manually and aligned by ClustalW algorithm (Thompson et al. 1994) in MEGA version 5 (Tamura et al. 2011). The alignment was checked again and all sites were unambiguously aligned. The best evolutionary model of nucleotide substitution for our dataset was established by Akaike Information Criterion, performed with jModelTest (Guindon and Gascuel 2003; Posada 2008). For the maximum likelihood (ML) analysis the Hasegawa-Kishino-Yano model (Hasegawa et al. 1985) with gamma distributed rate heterogeneity (HKY + G) was selected. Neighbour joining (NJ) analysis used the Tamura-Nei model (Tamura and Nei 1993) with uniform rates (TN). Maximum parsimony (MP) analysis was conducted using a heuristic search option and default options (TBR branch swapping, ACCTRAN character state optimisation), with the exception of using random stepwise addition repeated 100 times. All phylogenetic and molecular evolutionary analyses were conducted using MEGA version 5 (Tamura et al. 2011). Five hundred bootstrap replicates were performed to obtain a relative measure of node support for the resulting trees. Average pairwise NJ distances for each dataset were also computed in MEGA version 5 using the Tamura-Nei model. All trees were rooted with *Schizopera leptafurca* Karanovic & Cooper, 2012 from Western Australia, its mtCOI sequences also available from GenBank prior to this study [JQ390578.1], which belongs to the subfamily Diosaccinae Sars, 1906 of the family Miraciidae Dana, 1846.

Systematics

Subphylum Crustacea Brünich, 1772

Class Maxillopoda Dahl, 1956

Subclass Copepoda H. Milne Edwards, 1840

Order Harpacticoida Dana, 1846

Family Miraciidae Dana, 1846

Subfamily Stenheliinae Brady, 1880

Genus *Stenhelia* Boeck, 1865

Stenhelia pubescens Chislenko, 1978

http://species-id.net/wiki/Stenhelia_pubescens

Figs 1–7

Synonymy. *Stenhelia (Stenhelia) pubescens* Chislenko, sp. n. – Chislenko 1978: p. 173, Figs 9–11.

Type locality. Russia, Primorsky Krai, Sea of Japan, Posyet Bay, Minonosok inlet, benthic sands at 3–4 m depth, 42.609258°N, 130.861661°E.

Specimens examined. Two females (one ovigerous) together on one SEM stub (collection number NIBRIV0000232715), one female dissected on one slide (collection number NIBRIV0000232716), one female in ethanol (collection number NIBRIV0000232717), and two ovigerous females destroyed for DNA sequences (GenBank accession nos. KF524870 & KF524871); all from type locality, 6 May 2012, leg. Y. Trebukhova.

Redescription of female. Total body length, measured from tip of rostrum to distal margin of caudal rami, from 558 to 583 μm ($n = 6$). Colour of preserved specimens yellowish; live specimens not observed. Nauplius eye not visible. Several filamentous bacterial colonies in various places, some resembling sensilla (see Fig. 1C). Prosome comprising cephalothorax with completely fused first pedigerous somite, and three free pedigerous somites; urosome comprising first urosomite (= fifth pedigerous somite), genital double-somite (fused genital and third urosomites) and three free urosomites (last one being anal somite). Short sclerotized joint between prosome and urosome only discernible on ventral side. Habitus (Figs 1A, 2A) robust, spindle shaped in dorsal view, widest at posterior end of cephalothorax and tapering posteriorly, boundary between prosome and urosome conspicuous; prosome/urosome length ratio about 1.2, but prosome much wider and more voluminous. Body length/width ratio about 2.9; cephalothorax 1.65 times as wide as genital double-somite. Free pedigerous somites without lateral or dorsal expansions, pleurons only partly covering coxae of legs in lateral view (Fig. 1C). Integument of all somites relatively weakly sclerotized, generally very smooth, without cuticular windows or pits. Hyaline fringe of all somites broad and smooth, except for fourth pedigerous somite with narrow fringe dorsally, and for anal somite without hyaline fringe. Surface ornamentation of somites and caudal rami consisting of three unpaired dorsal pores, 61 paired pores and sensilla, and posterior row of spinules on last four urosomites only.

Rostrum (Figs 1B, 2B, 3C) large, trapezoidal, clearly demarcated at base, reaching midlength of second antennular segment, with bilobate tip, about as long as wide, with smooth dorsal surface and central keel on ventral surface, with two large lateral sensilla near tip inserted into deep recesses.

Cephalothorax (Figs 1B, 2A, B, D) tapering anteriorly in dorsal view, about as long as wide; comprising 35% of total body length. Surface of cephalothoracic shield with three pairs of small pores near antero-ventral corner between antennula and antenna (Fig. 2B), one dorsal unpaired pore in anterior half, and 25 pairs of long sensilla (Fig. 1B); of those only eight pairs of sensilla belonging to first pedigerous somite incorporated into cephalothorax (Figs 1B, 2D)

Pleuron of second pedigerous somite (first free) (Fig. 1C) with nearly rectangular lateral section, without pores but with seven pairs of large sensilla, two of them near lateral margin; serial homologies with sensilla on posterior part of cephalothorax (belonging to first pedigerous somite) difficult to define, except perhaps for anterior lateral sensilla and two other posterior pairs.

Pleuron of third pedigerous somite (Fig. 1C) somewhat shorter than that of second pedigerous somite and with slightly more rounded lateral section, but also with no pores and with seven pairs of large sensilla; recognising sensilla serially homologous to those on pleuron of second pedigerous somite easy for all seven pairs.

Pleuron of fourth pedigerous somite (Fig. 1C) much shorter and with more rounded lateral section than those of previous two somites, especially narrow in dorsal view, with only five pairs of large sensilla; serial homology of sensilla to those on two previous somites relatively difficult to establish, but probably two dorsal pairs homologous to two dorsalmost pairs on pleuron of third pedigerous somite and two lateral pairs homologous to those near lateral margin on two previous somites.

First urosomite (Figs 1D, 3A, B) about as long and as wide as fourth pedigerous somite but with wider hyaline fringe, with only three dorso-lateral pairs of long sensilla and no pores or spinules.

Genital double-somite (Figs 1D, 3A, B) about 1.2 times as wide as long (ventral view); completely fused ventrally but with deep suture indicating original segmentation between genital and third urosomites dorso-laterally, thus dividing double-somite into equally long halves; anterior half of genital double-somite 1.2 times as wide as posterior, inflated laterally; anterior part with one unpaired dorsal pore and two pairs of long dorsal sensilla; serially homologous sensilla of anterior part of double-somite and those of first urosomite not easy to establish; posterior part with three pairs of posterior sensilla (one dorsal, one lateral, and one ventral) and long row of posterior dorso-lateral spinules of various length; establishing serially homologous sensilla of posterior and anterior part of double-somite not easy; hyaline fringe wider than in first urosomite. Female genital complex (Fig. 3B) weakly sclerotized and hardly distinguishable from internal sutures and soft tissue, copulatory pores not exposed on surface but their position could be deduced from attached spermatophores (Fig. 1D); paired genital apertures situated ventro-laterally, close to anterior margin and covered by reduced sixth legs.

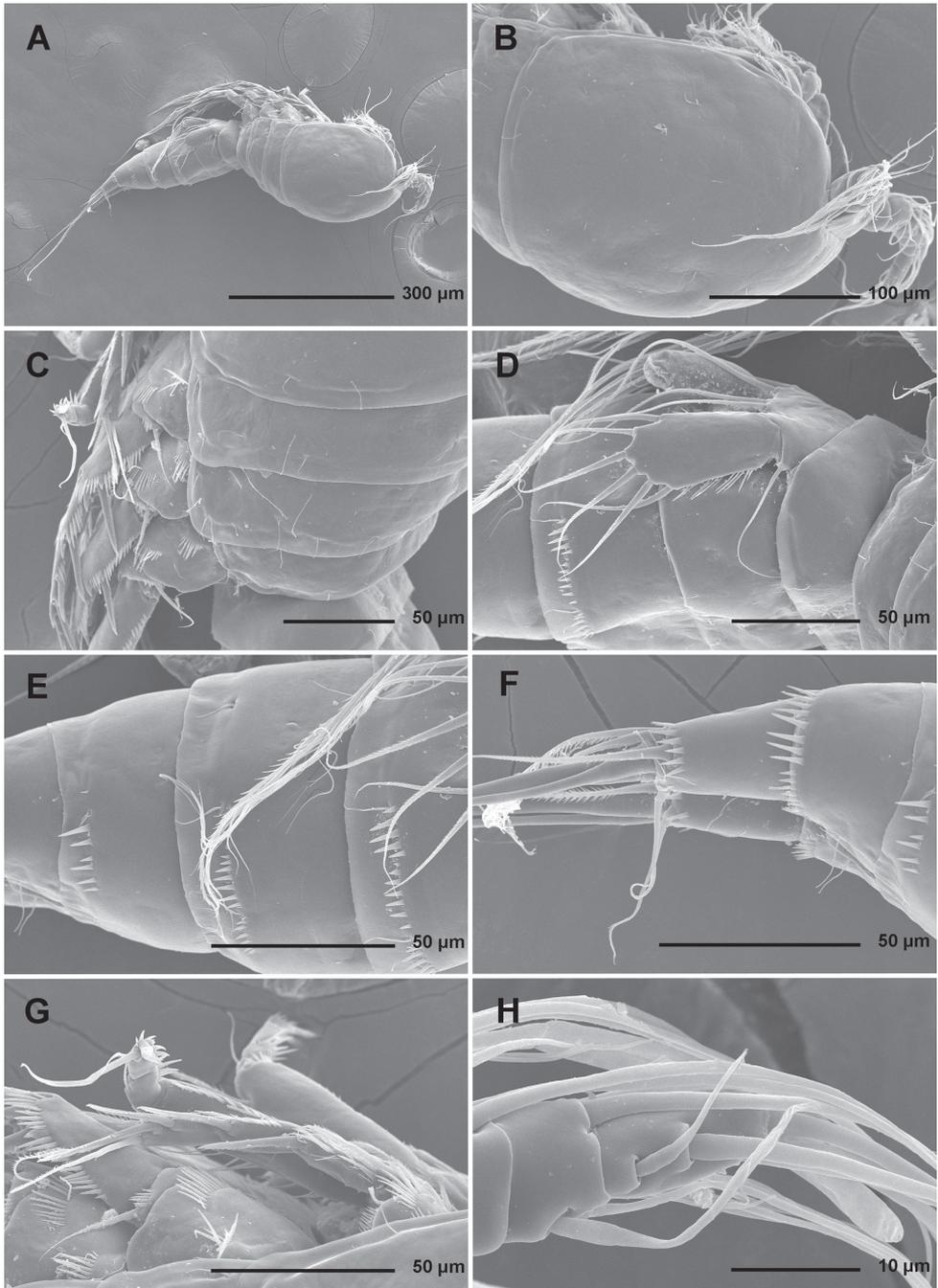


Figure 1. *Stenhelia pubescens* Chislenko, 1978, scanning electron micrographs, female 1: **A** habitus, lateral **B** cephalothorax, lateral **C** free thoracic somites, lateral **D** fifth pedigerous somite and genital double-somite, lateral, with one spermatophore attached on ventral side **E** fourth and fifth urosomites, lateral **F** anal somite and caudal rami, lateral **G** first legs and proximal part of second and third legs, lateral **H** distal part of right antennula, dorsal.

Third urosomite (Figs 1E, 3A, B) slightly narrower than posterior half of genital double-somite, but about as long and ornamented very similarly with three pairs of posterior sensilla and posterior row of spinules of various size, interrupted dorsally and ventrally; all sensilla with homologous pairs on posterior half of genital double-somite; hyaline fringe as wide as in genital double-somite.

Fourth urosomite (preanal) (Figs 1E, 3A, B) without sensilla or pores, only ornamentation posterior row of spinules with wider dorsal and ventral interruption than in previous two somites; hyaline fringe slightly narrower than in third urosomite.

Fifth urosomite (anal) (Figs 1F, 2G, 3A, B) clefted medially in posterior half, without anal operculum, with one pair of large dorsal sensilla, one pair of ventral pores, and posterior row of spinules at base of each caudal ramus; anal sinus with several diagonal rows of hair-like spinules on both sides of median cleft, widely open, with weakly sclerotised walls, and without chitinous projections.

Caudal rami (Figs 1F, 2G, H, 3A, B) short and slender, cylindrical, about as long as anal somite, 1.5 times as long as wide (dorsal view), slightly divergent, with space between them about one ramus width; armature consisting of seven setae (three lateral, one dorsal and three apical), all in posterior sixth of ramus length; ornamentation consisting of one ventral pore at midlength, one posterior ventral tubular pore, several spinules at base of each lateral seta and at base of dorsal seta, and two large posterior ventral spinules at base of innermost apical seta. Dorsal seta slender, plumose at distal tip, inserted close to inner margin, about 1.2 times as long as caudal ramus, triarticulate at base (i.e. inserted on two pseudojoints). Lateral setae all bipinnate and unarticulate; ventralmost one longest and most slender, with distal tuft of longer pinnules, inserted very close to distal margin, about 1.3 times as long as caudal ramus; dorsalmost one strongest, without distal tuft of long pinnules, about 0.8 times as long as ventralmost one, inserted slightly more anteriorly than ventralmost one, at about same level as dorsal seta; central one half as long as dorsalmost one, also strong, inserted at about same level, also without distal tuft of long pinnules. Inner apical seta only slightly shorter than ventralmost lateral seta but very similar in thickness and ornamentation, i.e. also with distal tuft of long pinnules. Principal apical setae not fused basally, both with breaking planes; middle apical seta much stronger and longer, about 2.2 times as long as outer apical one, bipinnate; outer apical seta smooth, about 3.8 times as long as caudal ramus.

Antennula (Figs 1H, 2B, 5A) eight-segmented, joined to cephalothorax with small triangular cuticular plate, about half as long as cephalothorax, with single short anterior row of spinules on first segment. Fourth segment sometimes with suture along caudal margin. Distal caudal corner of first segment not produced. Long aesthetasc on fourth segment slender, fused basally with adjacent large seta, and reaching beyond tip of appendage; slender short apical aesthetasc on eighth segment fused basally with two apical setae, forming apical acrothek. Setal formula: 1.11.9.6+ae.3.4.4.6+ae. All setae smooth, dorsalmost setae on second segment with breaking plane, two caudal setae on seventh segment and four caudal setae on eight segment biarticulate. Length ratio of antennular segments, measured along caudal margin, 1 : 0.4 : 0.3 : 0.4 : 0.3 : 0.4 : 0.4 : 0.5.

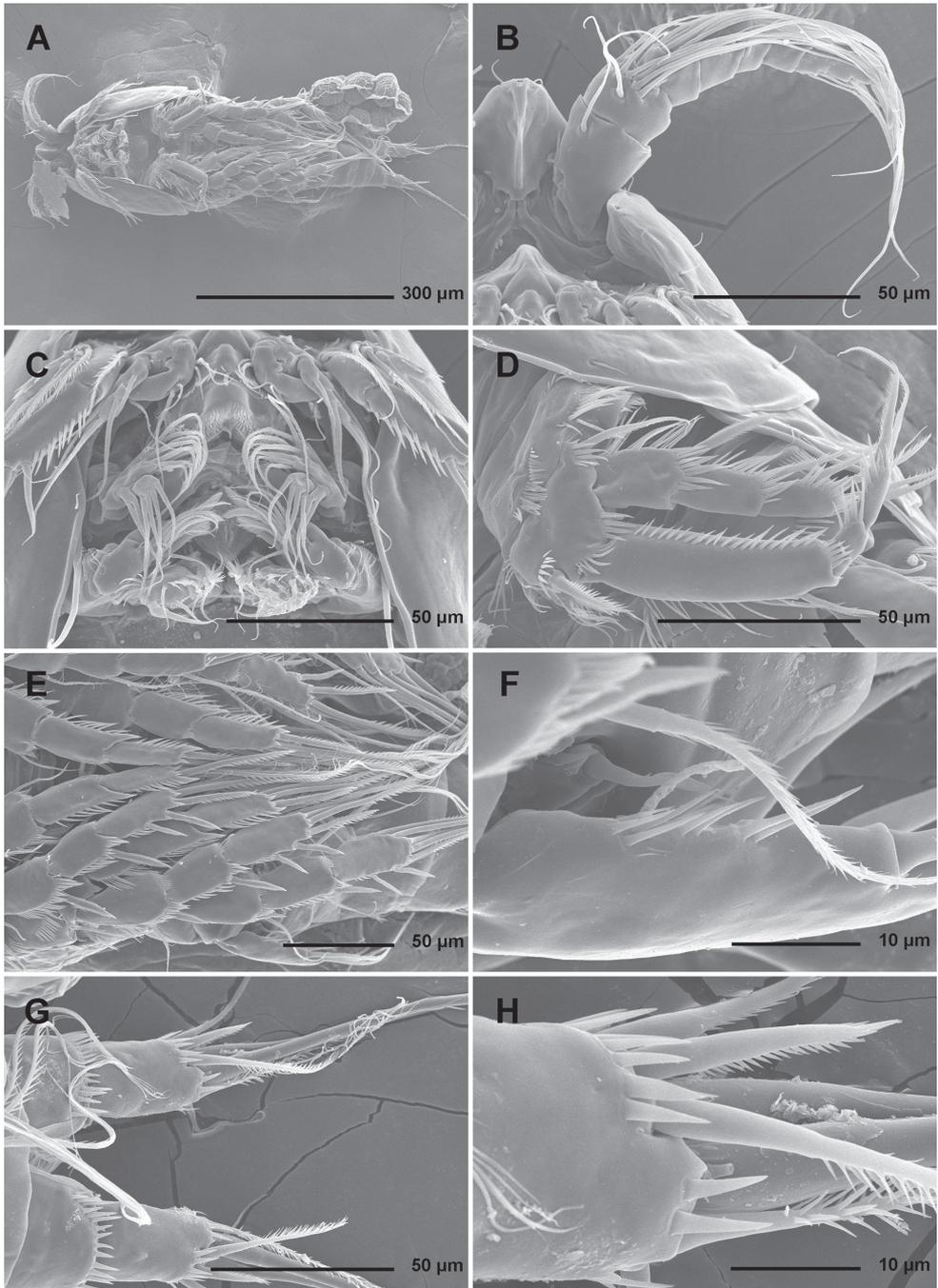


Figure 2. *Stenhelia pubescens* Chislenko, 1978, scanning electron micrographs, ovigerous female 2: **A** habitus, ventral **B** rostrum and left antennula, ventral **C** mouth appendages, ventral **D** first leg, anterior **E** second, third, and fourth legs, anterior **F** exopod of fifth leg and sixth leg, ventral **G** anal somite and caudal rami, ventral **H** posterior part of left caudal ramus, ventral.

Antenna (Figs 2C, 5B, C) relatively short, composed of coxa, allobasis, one-segmented endopod and three-segmented exopod. Coxa short, with arched row of long posterior spinules. Allobasis with smaller or bigger suture marking ancestral division between basis and first endopodal segment, most robust segment of antenna, more than four times as long as coxa and about as long as endopod, widest at base and about 2.5 times as long as wide, with single unipinnate inner seta at about midlength and several longer and smaller spinules in proimal half. Endopod about as wide as distal part of allobasis, almost cylindrical, about 3.6 times as long as wide, with two surface frills subdistally, row of large spinules all along anterior margin, two lateral spines flanking two thin setae, apical armature consisting of seven pinnae setae (four strong, long, and geniculate, innermost one strong but short, and two short and slender); two caudal-most setae fused basally. Exopod long and slender, almost cylindrical, about as long as allobasis but only half as wide; armature formula 1.1.4 and length ratio of segments 1 : 0.3 : 1.1; proximal segment with transverse distal row of small anterior spinules, bearing a unipinnate seta close to distomedial corner; second segment unornamented, with a unipinnate setae at distomedial corner; distal segment with two parallel longitudinal anterior rows of small spinules joining at distal margin, with one bipinnae inner seta, at about first third of its length, and three apical slender (two smooth and one bipinnate).

Labrum (Fig. 2C) large and complex tri-dimensional structure, trapezoidal in anterior view, rigidly sclerotized, with relatively wide convex cutting edge, subapically and apically with several rows of short slender spinules, with one additional transverse row of small anterior spinules and another patch of small posterior spinules.

Paragnaths (Fig. 2C) also forming complex tri-dimensional structure, trilobate, with two ellipsoid anterior lobes and one central, much shorter posterior lobe, all lobes fused at base; anterior lobes with one long row of slender spines along inner margin and one additional and parallel row of stronger spinules on anterior surface; posterior (central) lobe similar in shape and ornamentation to distal part of labrum but much smaller.

Mandibula (Figs 2C, 4A) with wide cutting edge on relatively short coxa, with three strong bicuspidate teeth ventrally, eight smaller unicuspidate teeth dorsally, and single unipinnate dorsalmost seta; seta fused basally to neighbouring tooth and twice as long as it; only ornamentation on coxa short row of six slender posterior spinules. Palp biramous, comprising basis, one-segmented exopod, and one-segmented endopod. Basis with somewhat inflated central part, about 2.5 times as long as wide, with three slender but pinnate distal outer setae, and with three transverse rows of strong spinules, distalmost one with strongest spinules. Exopod 0.6 times as long as basis and less than half as wide, narrowest medially, curved back towards coxa and almost parallel with basis, with three lateral and five apical setae; all lateral and three apical setae slender, two apical setae strong and geniculate, longer one of them almost four times as long as exopod; two apical setae unipinnate, all other exopodal setae smooth. Endopod 0.8 times as long as exopod, 3.8 times as long as wide, with one inner, three apical, and two outer slender setae; inner seta bipinnate, proximal outer and inner apical setae unipinnate, others smooth.

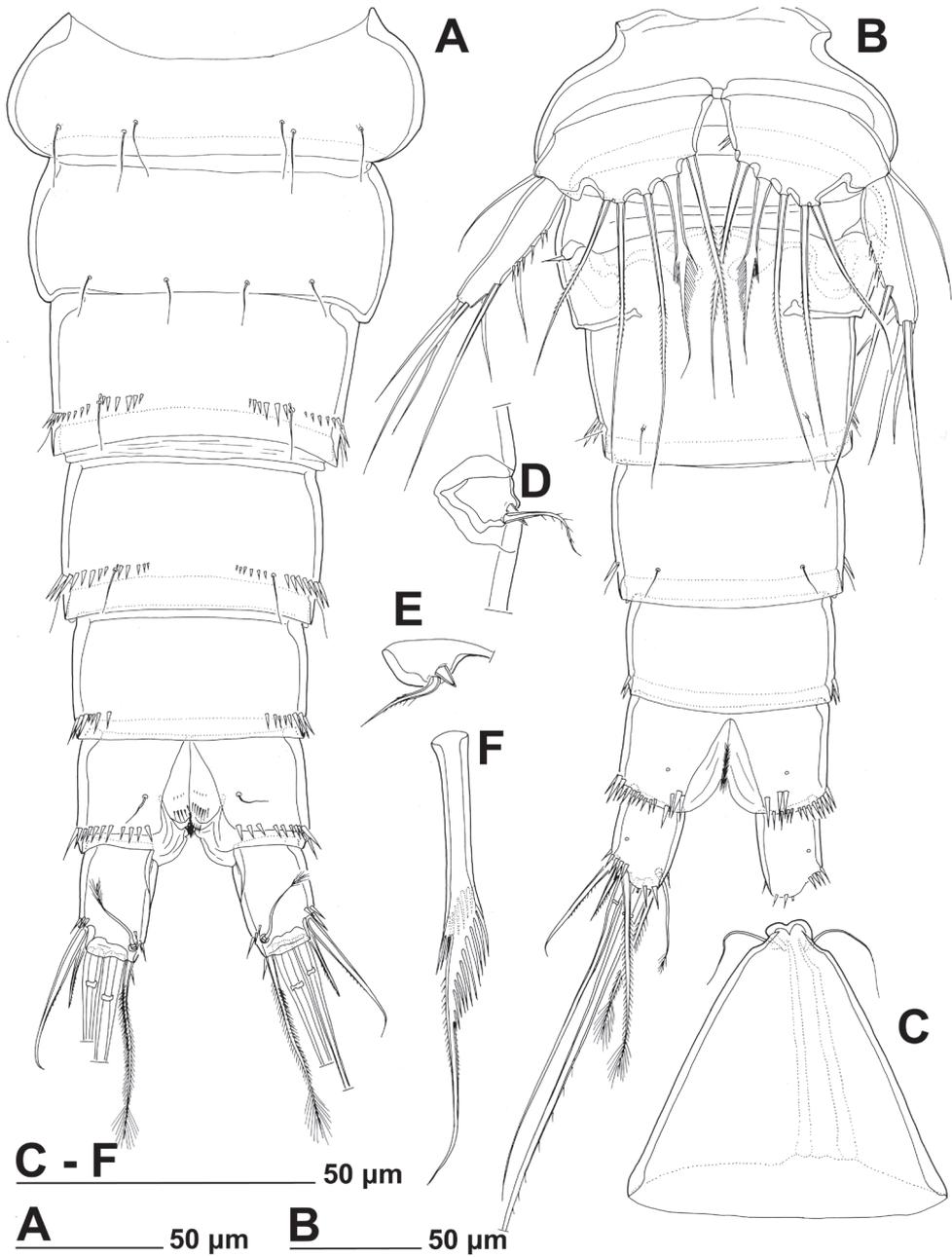


Figure 3. *Stenhelia pubescens* Chislenko, 1978, line drawings, female 3: **A** urosome, dorsal **B** urosome, ventral (armature on left caudal ramus omitted) **C** rostrum, dissected and compressed, dorsal **D** sixth leg, dorso-lateral **E** sixth leg, ventro-lateral **F** fifth leg second endopodal seta from inner side, anterior.

Maxillula (Figs 2C, 4C, D) composed of praecoxa, coxa, basis, one-segmented endopod, and one-segmented exopod; endopod and exopod fused basally. Praecoxa large; arthrite rectangular, without spinules, with nine strong curved spines apically and subapically, all except ventralmost spine with dense tuft of distal spinules along convex margin; dorsalmost spine on praecoxal arthrite longest, ventralmost one shortest. Coxa with anterior arched row of short spinules, endite shorter than praecoxal arthrite, with three slender pinnate apical (on inner margin) setae. Basis wider and longer than coxa, with two endites, with dorsal row of strong spinules and three unipinnate setae on dorsal endite, and another three unipinnate setae on ventral endite. Endopod minute, rectangular, with four slender bipinnate apical setae. Exopod smaller than endopod, with two slender bipinnate apical setae.

Maxilla (Figs 2C, 4E) composed of large syncoxa, small basis and even smaller one-segmented endopod. Syncoxa with four rows of outer long spinules and with three endites; dorsal endite smallest, with one subapical and two apical strong pinnate setae; central and ventral endites slender, with three apical pinnate setae each, setae on ventral endite longest; two distal rows of spinules parallel on anterior surface, two proximal rows of spinules near outer margin, one on anterior, one on posterior surface, posterior distal surface smooth. Basis slightly larger than ventral endite of syncoxa, with anterior row of minute spinules, apically with two strong and geniculate, unipinnate spines, and two slender setae on ventral and posterior surfaces. Endopod much smaller than basis, twice as long as wide, with basal tubular pore, no spinules, with three lateral and three apical slender setae of similar length; two lateral setae unipinnate, others smooth.

Maxilliped (Figs 2C, 4F) prehensile, four-segmented, composed of coxa, basis, and two-segmented endopod. Coxa short, almost triangular, unarmed and unornamented. Basis largest and longest segment, about 1.8 times as long as wide and nearly five times as long as coxa, with one arched posterior row and two longitudinal anterior rows of slender spinules, with three strong unipinnate distomedial setae of about same length. First endopodal segment 0.8 times as long as basis but slightly wider, almost ovoid in shape, also with one posterior and two anterior rows of spinules but spinules much longer and stronger, with two smooth distomedial setae, one of them slightly longer and considerably stronger. Second endopodal segment minute, nearly rectangular, 1.6 times as long as wide, 0.4 times as long as first endopodal segment, unornamented, with apical strong prehensile smooth spine, and with subapical shorter and much more slender, unipinnate seta.

All swimming legs (Figs 1A, 2A) of similar size and long in comparison to body length, composed of small triangular and unarmed praecoxa, large rectangular and unarmed coxa, shorter and nearly pentagonal basis, slender three-segmented exopod, and slender three-segmented endopod; pair of legs joined by simple intercoxal sclerite.

First leg (Figs 1G, 2D, 5D) with smooth and short intercoxal sclerite, its distal margin nearly straight. Praecoxa longer than wide, longer than intercoxal sclerite but shorter than coxa, unornamented. Coxa 1.8 times as wide as long, with longitudinal row of long and slender inner spinules, three transverse rows of shorter but stronger

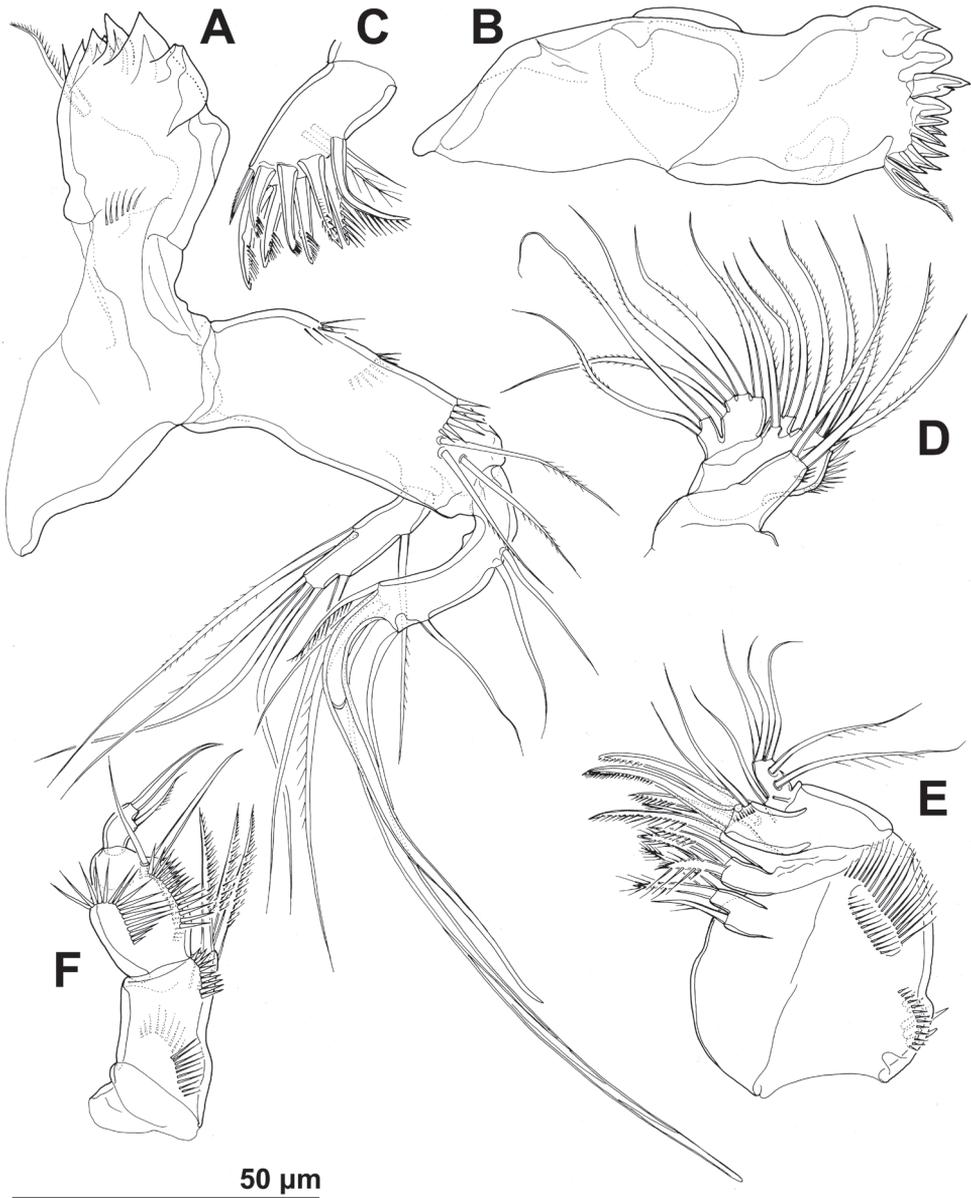


Figure 4. *Stenhelia pubescens* Chislenko, 1978, line drawings, female 3: **A** mandibula, posterior **B** mandibular coxa, anterior **C** maxillula, praecoxa arthrite, posterior **D** maxillular palp, posterior **E** maxilla, anterior **F** maxilliped, anterior.

anterior spinules, and two short rows of even smaller posterior spinules. Basis with one long strong and finely bipinnate outer spine, one shorter but stronger bipinnate inner spine, and four transverse rows of large anterior spinules (one at base of each spine, one at base of endopod, and one on proximal inner corner; latter with longest spinules).

Exopod with all segments of similar length, each about twice as long as wide and with strong outer spinules and subdistally on anterior surface; first segment with anterior pore near distal outer corner; second segment with slender inner spinules; first two segments with single strong and finely bipinnate distolateral spine; third segment with two strong and finely bipinnate outer spines and two slender and finely bipinnate apical setae; apical setae not prehensile; length ratio of elements on third segment, starting from outer margin, 1 : 1.4 : 2 : 2.4. Endopod three-segmented, prehensile, about 1.4 times as long as exopod; first endopodal segment about as long as entire exopod and 3.3 times as long as wide, with slender and long inner spinules, shorter and stronger outer and anterodistal spinules, with single bipinnate inner seta, the latter slender and about 0.4 times as long as segment; second segment small, rhomboidal, slightly longer than wide and only one sixth of first segment's length, with several strong anterodistal spinules, and single slender and bipinnate inner seta; latter about 1.6 times as long as segment; third segment about 2.5 times as long as wide and 1.4 times as long as second segment, with several strong inner spinules and three smaller antero distal spinules, with one slender inner seta, one strong and long apical seta, and another shorter and stronger outer apical spine; apical spine 1.7 times as long as third segment, half as long as apical seta, and 1.5 times as long as inner seta on third segment; longest seta on exopod and endopod of about same length.

Second leg (Figs 1G, 2E, 6A), intercoxal sclerite about as long as wide, unornamented, with two sharp and inwardly pointed distal processes. Praecoxa very short, unornamented. Coxa nearly 1.5 times as wide as long, with anterior pore near distomedial corner, three short rows of strong anterior spinules (one at distomedial corner, one near proximal outer corner, and one near distal outer corner), and two short rows of minute anterior spinules. Basis with nearly smooth (minute pinnules barely visible), short and slender outer spine; inner distal corner produced into long and sharp process directed inwardly, another smaller distal process between exopod and endopod; with transverse row of long anterior spinules near inner margin, several smaller spinules at base of outer spine, and discontinuous row of minute spinules at base of endopod. First exopodal segment widest, third segment slender and about 2.3 times as long as wide, 1.4 times as long as second segment, and about as long as first one; first and second segment with strong outer and anterodistal spinules and with distomedial frills, third segment with several outer strong spinules in proximal half and with anterior pore; first and second segments with single strong and finely bipinnate outer distal spine and slender bipinnate inner distal seta; third segment with three strong finely bipinnate outer spines, two apical strong bipinnate setae, and one slender bipinnate inner seta; inner apical seta on third segment longest, about 1.2 times as long as outer apical one, 2.4 times as long as third segment, and 2.7 times as long as outer distal spine; outer distal corner of first and second segment produced into small spiniform process. Endopod about as long as exopod; all segments of about same length, but progressively narrower from proximal to distal end, each with outer distal corner produced into strong spiniform process (first segment also with distomedial smaller process), and each with row of strong outer spinules, first

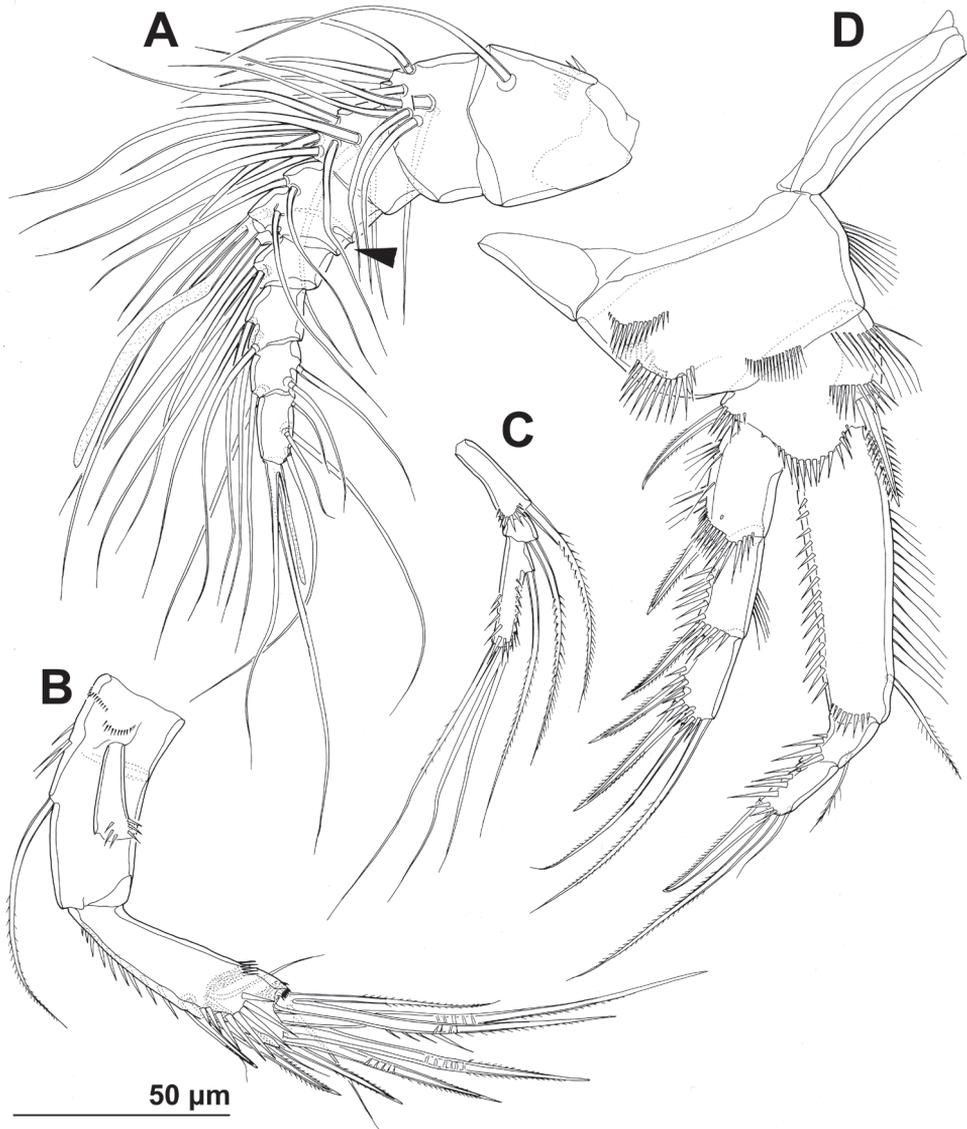


Figure 5. *Stenhelia pubescens* Chislenko, 1978, line drawings, female 3: **A** antennula, ventral **B** basis, endopod, and first exopodal segment of antenna, anterior **C** antennal exopod, anterior **D** first leg, anterior. Arrowhead indicates the presence of caudal suture on the fourth antennular segment.

two segments additionally with small distomedial frills, and first and third segments with anterior cuticular pore; armature consisting of single bipinnate inner seta on first segment, two pinnate slender inner setae on second segment, and one inner and three apical elements on third segment (probably outermost spine and two strong setae); seta on first segment about as long as segment, those on second segment about

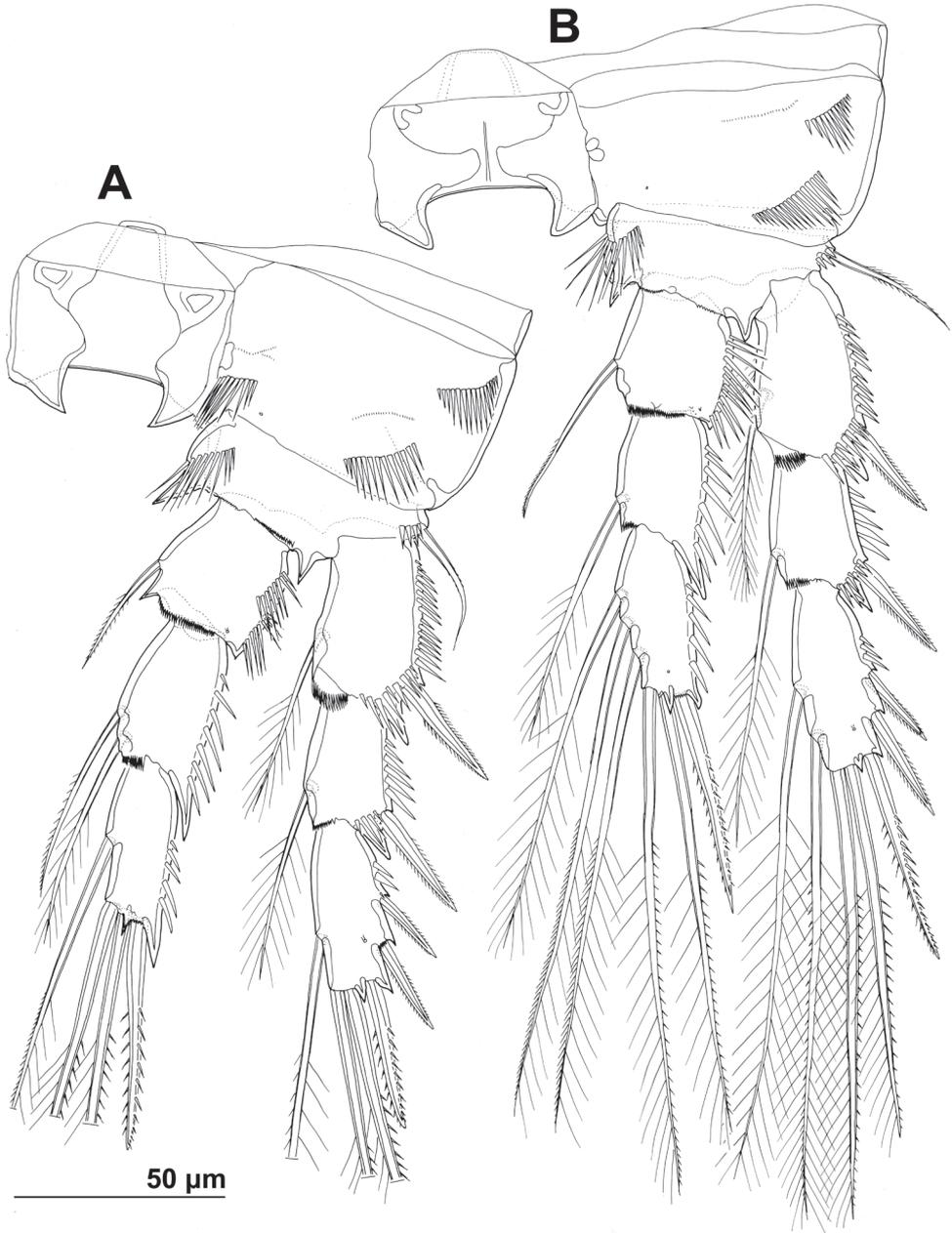


Figure 6. *Stenbelia pubescens* Chislenko, 1978, line drawings, female 3: **A** second leg, anterior **B** third leg, anterior.

1.4 times as long as segment, and those on third segment about twice as long as segment, except outer spine, which is about 1.4 times as long as segment. Two apical exopodal and endopodal setae each with shorter and stronger outer pinnules, inner

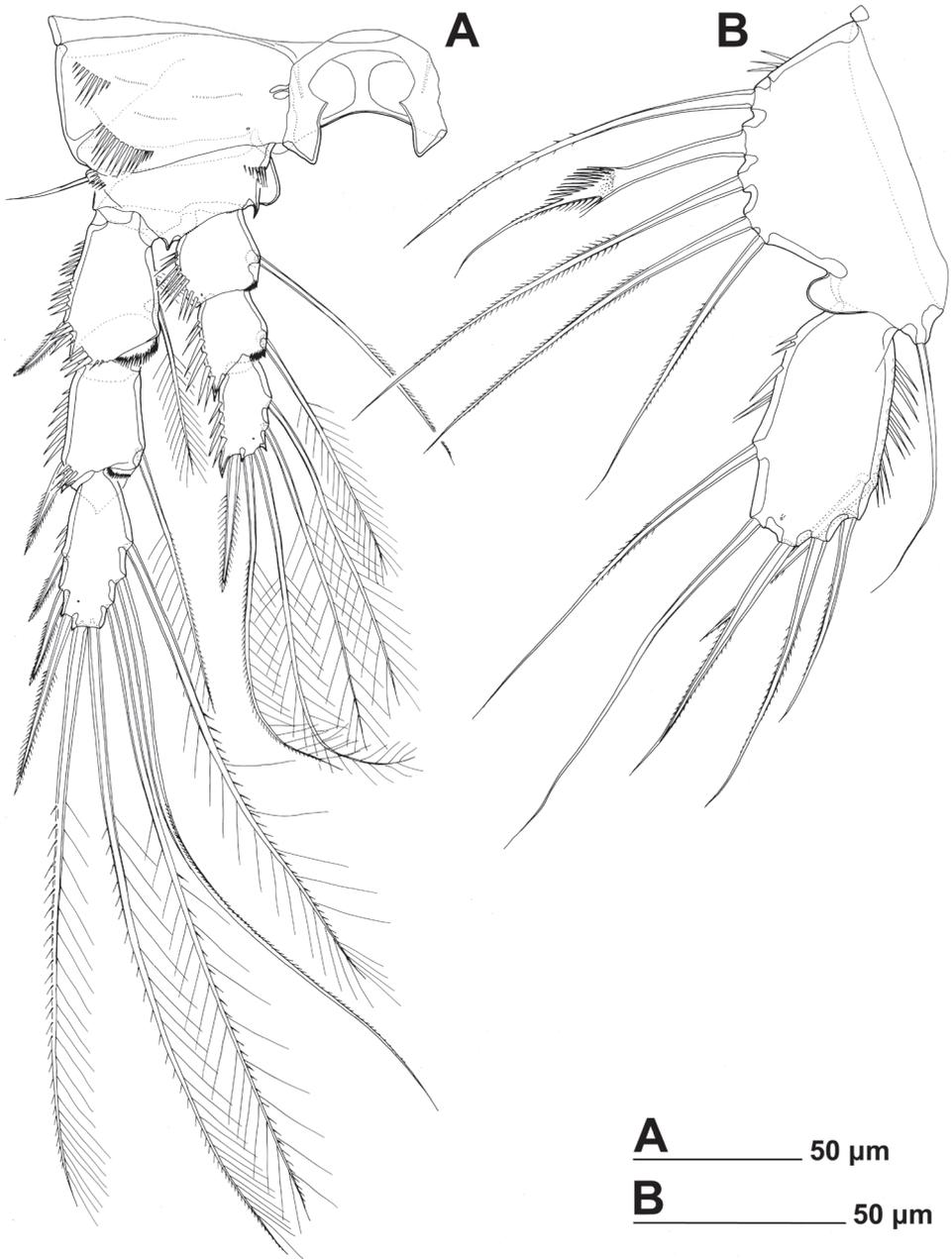


Figure 7. *Stenhelia pubescens* Chislenko, 1978, line drawings, female 3: **A** fourth leg, anterior **B** fifth leg, dissected and flattened, anterior.

setae on third exopodal and endopodal segments and proximal inner seta on second endopodal segment with shorter inner pinnules, all other bipinnate setae and spines with symmetrical pinnules.

Third leg (Figs 2E, 6B) similar to second leg, except for slightly less sharp processes on intercoxal sclerite, absence on distomedial row of strong spinules on coxa, smaller spiniform distomedial process on basis, two inner setae on third exopodal segment, one inner seta on second endopodal segment, and three inner seta on third endopodal segment; proximal inner seta on third endopodal and exopodal segment with long pinnules on both sides, distal inner seta on third exopodal segment with short pinnules on inner margin in addition to long ones, other setae and spines as in second leg.

Fourth leg (Figs 2E, 7A) relatively similar to third leg, but with endopod only about 0.6 times as long as exopod, with slightly shorter distomedial process on basis, much longer seta on first endopodal segment, only two inner setae on third endopodal segment, and three inner setae on third exopodal segment; central inner seta on third exopodal segment spiniform and characteristically curved inwards; all setae on third exopodal segment proportionately longer than in second or third leg.

Fifth leg (Figs 1D, 2F, 3B, F, 7B) composed of wide baseoendopod (fused basis and endopod) and much smaller and almost ovoid exopod, pair of legs joined by minute trapezoidal sclerite. Baseoendopod about 1.8 times as wide as long, more or less pentagonal, unornamented, with short and blunt process at base of exopod; outer basal seta slender and smooth, arising from short setophore, about 1.6 times as long as segment; endopodal lobe relatively narrow and short, more or less trapezoidal, not extending beyond proximal fifth of exopod, with five stout, bipinnate setae, their length ratio, starting from inner side, 1 : 0.8 : 1.2 : 1 : 0.8. Second endopodal seta from inner side with stout and smooth proximal half, characteristic transverse serrate comb near mid-length, and distal slender finely bipinnate whip; whip about as long as proximal part of seta. Exopod about 2.1 times as long as its maximum width, more or less ovoid, with narrower base than rest of it, with strong outer and inner spinules and single anterior pore close to distal margin, with six setae; innermost and second inner seta slender, others shorter and spiniform, second seta from inner side smooth, other setae bipinnate; length ratio of exopodal setae, starting from inner side, 1 : 1 : 1.4 : 1.4 : 0.6 : 0.6.

Sixth leg (Figs 2F, 3B, D, E) minute flap covering ventro-lateral genital aperture, mostly fused to somite, unornamented, with single short bipinnate seta near outer margin and one minute inner spine. Sixth legs seemingly joined on ventral side by fold-like suture which hides copulatory pores.

Variability. Most morphological features in examined topotypes were conservative, including the sensilla and pores pattern on somites, and length ratio of different armature on appendages. The only significant form of morphological variability, except for the body length, was presence/absence of caudal suture on the fourth antennular segment (compare Figs 2B and 5A; arrowed in Fig. 5A) and the size of suture on the antennar allobasis indicating remnants of ancestral arthroidal membrane (Fig. 5B). We redescribe this species in order to show some previously unreported characters, so they can be compared with those of *Stenbelia taiae*. Differences from the original description of Chislenko (1978) are given in the Discussion section below.

***Stenhelia taiae* Mu & Huys, 2002**

http://species-id.net/wiki/Stenhelia_taiiae

Figs 7–12

Synonymy. *Stenhelia taiae* sp. n. – Mu and Huys 2002, p. 187, Figs 10–13.

Type locality. China, Bohai Sea, central region, sandy and muddy sediments at about 20 m depth, approximately 38.5°N, 120°E.

Specimens examined. One female on one SEM stub (collection number NI-BRIV0000232718), one female dissected on one slide (collection number NI-BRIV0000232719), and two females destroyed for DNA sequences (GenBank accession nos. KF524885 & KF524884); all from South Korea, South Sea, Gwangyang Bay, sampling station 16, muddy sediments at about 10 m depth, 34.768889°N 127.783806°E, 18 November 2012, leg. K. Kim.

Redescription of female. Body length from 565 to 578 μm ($n = 4$). Body segmentation, colour, nauplius eye, hyaline fringes, integument thickness and surface appearance as in *Stenhelia pubescens*, including very smooth integument on all somites and their posterior frills. Most somite ornamentation also similar to *S. pubescens*, and homologous pores and sensilla easy to establish. Habitus (Fig. 8A) slightly less robust, with proportionately longer urosome (arrowed in Fig. 8A), prosome/urosome length ratio less than 1.1, body length/width ratio about 3.1, cephalothorax 1.6 times as wide as genital double-somite.

Rostrum (Figs 8H, 10D) slightly longer and narrower in dorsal view than in *S. pubescens* (arrowed in Fig. 10D).

Cephalothorax (Fig. 8B) about 0.9 times as long as wide; comprising about 30% of total body length, with posterior lateral corner slightly more rounded than in *S. pubescens*. Surface of cephalothoracic shield ornamented as in *S. pubescens*, except one anterior pair of lateral sensilla absent (arrowed in Fig. 8B) and one additional pair of anterior pores present (also arrowed in Fig. 8B).

Pleurons of second to fourth pedigerous somites (Fig. 8C) without any difference in shape or ornamentation from those in *S. pubescens*.

First urosomite (Figs 8D, 10A, B) with three pairs of long sensilla, as in *S. pubescens*, but with one additional short row of strong lateral spinules (arrowed in Fig. 8D).

Genital double-somite (Figs 8D, 10A, B) shape and most ornamentation as in *S. pubescens*, except anterior dorsal pair of sensilla more widely spaced (arrowed in Fig. 10A), posterior ventral pair of sensilla closer to each other (arrowed in Fig. 10B), and no spinules in between posterior dorsal pair of sensilla.

Third urosomite (Figs 8E, 10A, B) as in *S. pubescens*, except no spinules in between posterior dorsal pair of sensilla.

Fourth urosomite (Figs 8E, 10A, B) as in *S. pubescens*, except with fewer lateral spinules (arrowed in Fig. 8E).

Anal somite (Figs 8F, 10A, B) similar to that in *S. pubescens*, but additional pair of dorsal pores present, posterior spinules smaller and less dense, and medial cleft slightly narrower.

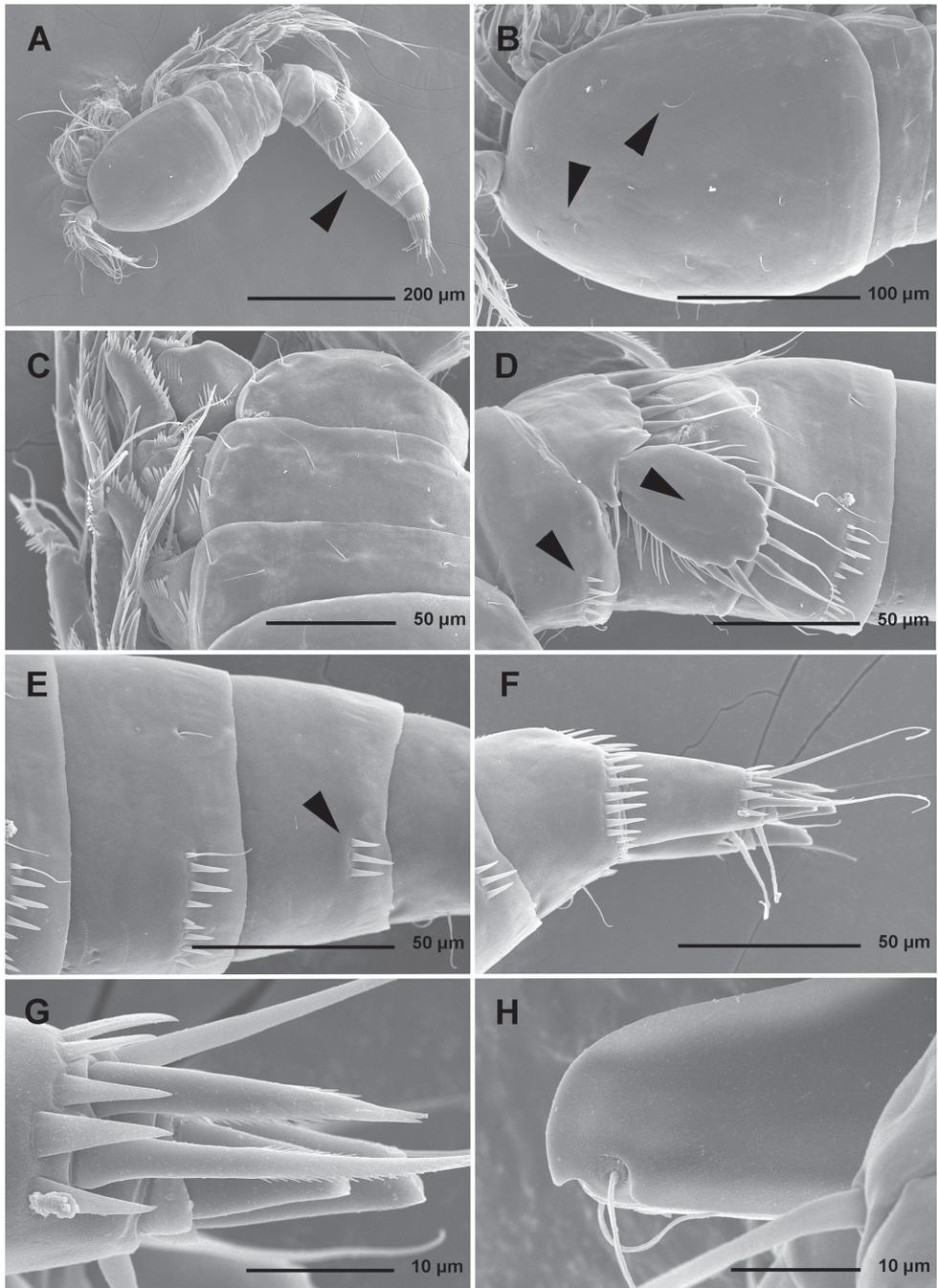


Figure 8. *Stenbelia taiiae* Mu & Huys, 2002, scanning electron micrographs, female: **A** habitus, lateral **B** cephalothoracic shield, lateral **C** free thoracic somites, lateral **D** fifth pedigerous somite and genital double-somite, lateral **E** fourth and fifth urosomites, lateral **F** anal somite and caudal rami, lateral **G** posterior part of right caudal ramus, lateral **H** rostrum, lateral. Arrowheads indicate morphological characters different from those in *S. pubescens* Chislenko, 1978.

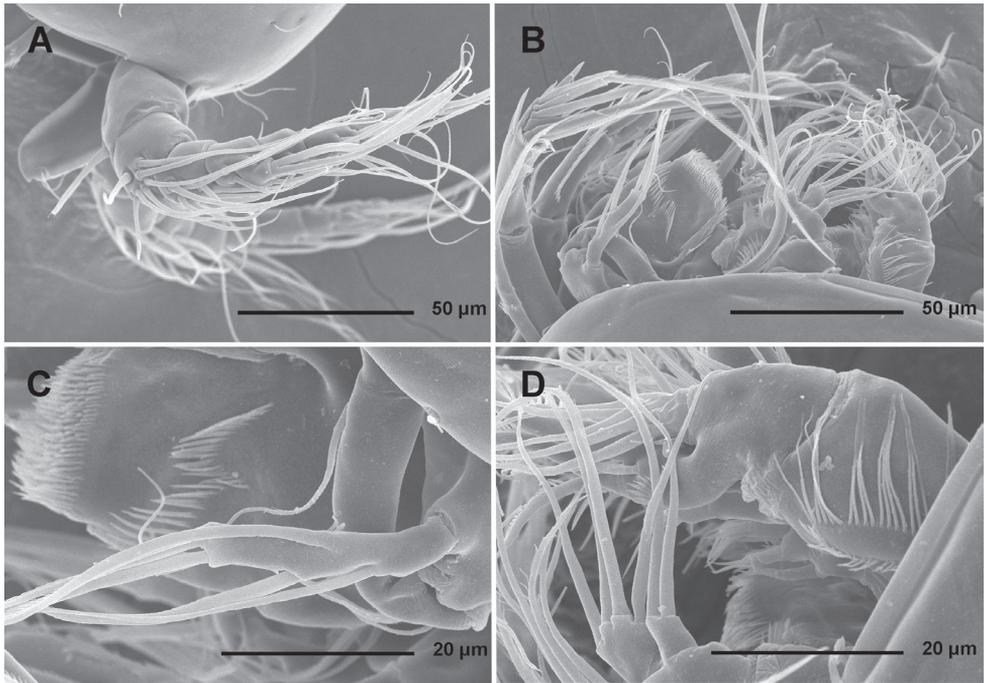


Figure 9. *Stenhelia taiiae* Mu & Huys, 2002, scanning electron micrographs, female: **A** rostrum and antennulae, lateral **B** antenna and mouth appendages, lateral **C** mandibular palp and labrum, lateral **D** maxilla and part of maxillular palp, lateral.

Caudal rami (Figs 8F, G, 10A, C), much longer than in *S. pubescens* (arrowed in Fig. 10A), about 1.3 times as long as anal somite, cylindrical, 2.1 times as long as wide (ventral view), slightly divergent, and with space between them about one ramus width; ornamentation and armature as in *S. pubescens*, except inner apical seta much shorter and smooth (arrowed in Fig. 10C), and ventralmost lateral seta smooth and slender; posteroventral tubular pore also present, but ventral pore at base of lateral setae situated at two thirds of ramus length, not at midlength.

Antennula (Fig. 9A), antenna (Fig. 9B), labrum (Figs 9C, 11A), paragnaths (Fig. 11B), mandibula (Fig. 9B, C), maxillula (Figs 9B, D, 11C), and maxilla (Figs 9D, 11D) as in *S. pubescens*.

Maxilliped (Fig. 11E) as in *S. pubescens*, except basal setae proportionately longer (arrowed in Fig. 11E) and apical endopodal spine proportionately shorter.

First leg (Figs 8A, C, 12A) as in *S. pubescens*, except first exopodal segment proportionately shorter, both basal spines proportionately longer, and coxa without posterior spinules (all four arrowed in Fig. 12A).

Second leg (Figs 8A, C, 12B) as in *S. pubescens*.

Third leg (Figs 8A, C, 12C) as in *S. pubescens*, except distomedial basal process slightly larger (arrowed in Fig. 12C).

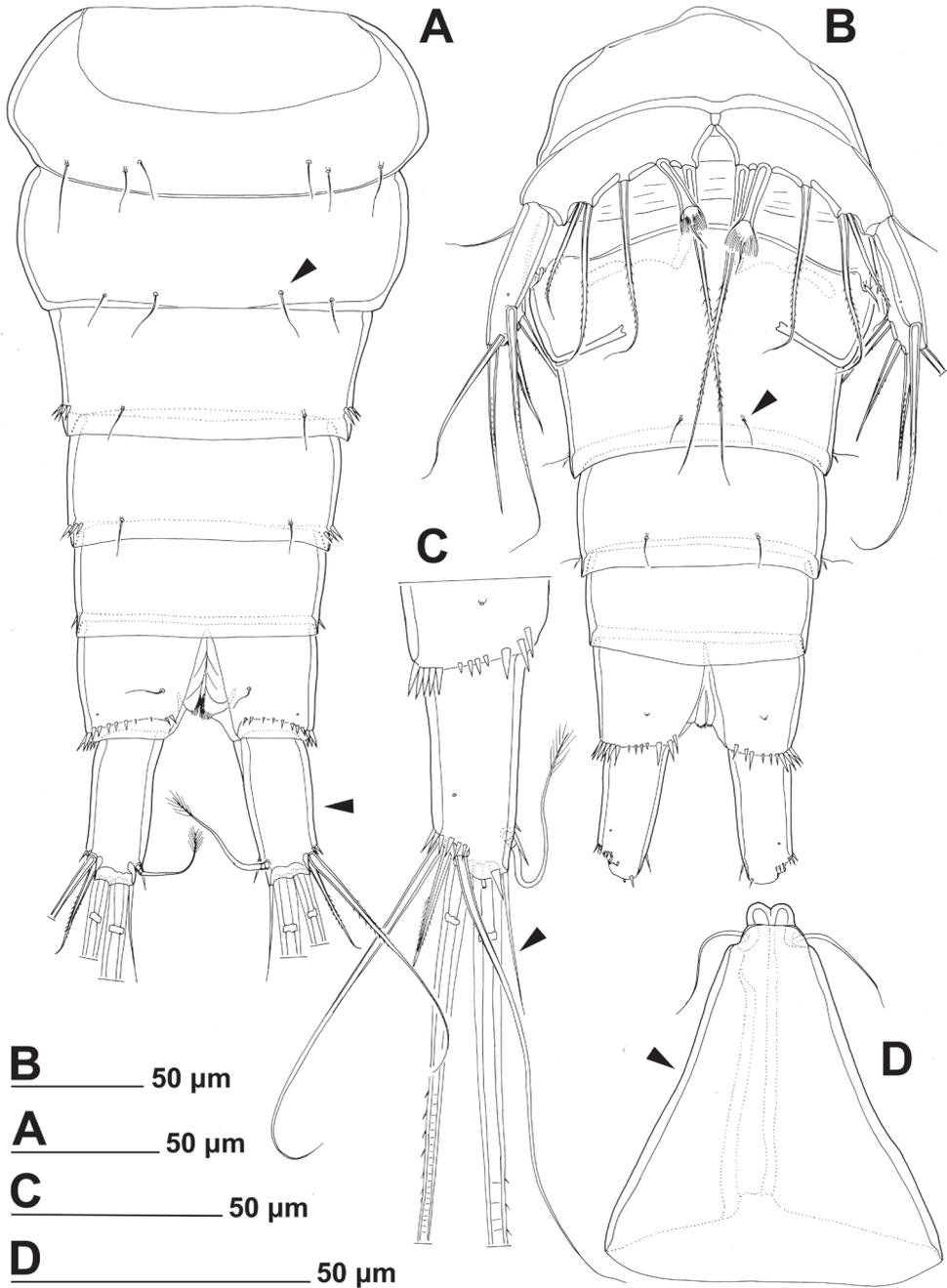


Figure 10. *Stenhelia taiiae* Mu & Huys, 2002, line drawings, female: **A** urosome, dorsal **B** urosome, ventral (caudal rami armature omitted) **C** right caudal ramus, ventral **D** rostrum, dissected and compressed, dorsal. Arrowheads indicate morphological characters different from those in *S. pubescens* Chisenko, 1978.

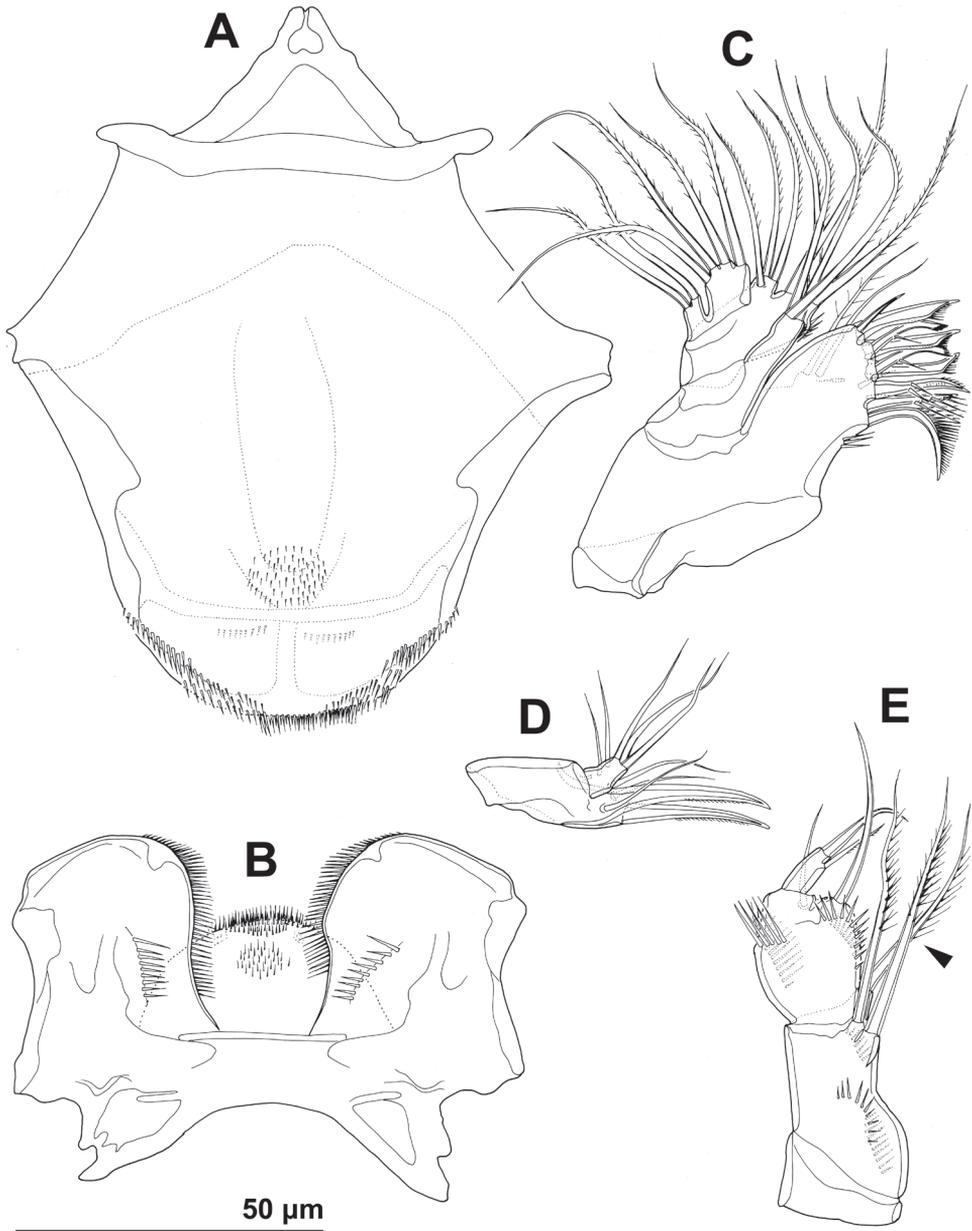


Figure 11. *Stenhelia taiae* Mu & Huys, 2002, line drawings, female: **A** labrum, posterior **B** paragnaths, anterior **C** maxillula, posterior **D** maxillar basis and endopod, posterior **E** maxilliped, posterior. Arrow-head indicates morphological character different from that in *S. pubescens* Chislenko, 1978.

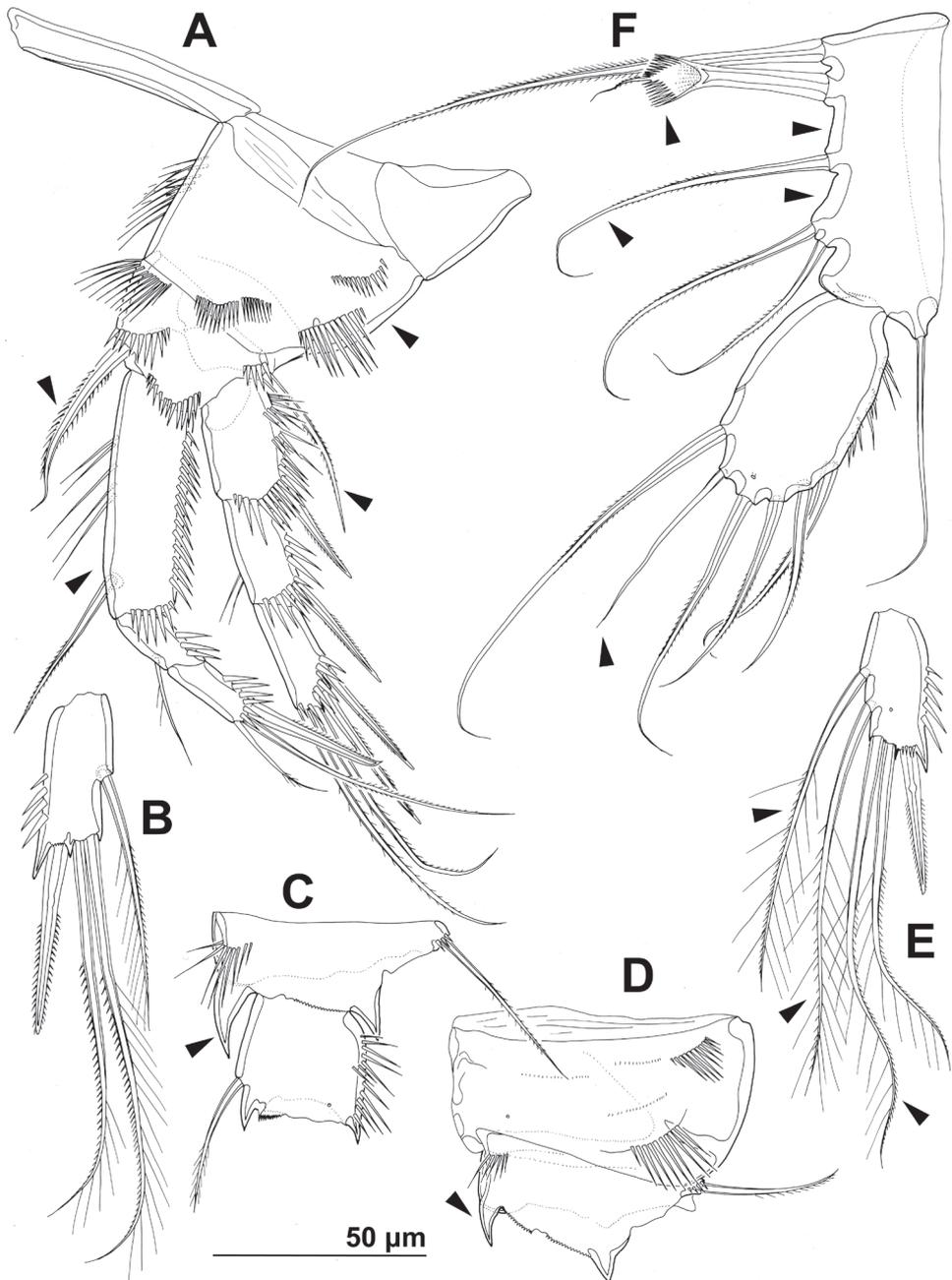


Figure 12. *Stenbelia taiiae* Mu & Huys, 2002, line drawings, female: **A** first leg, anterior **B** third endopodal segment of second leg, anterior **C** basis and first endopodal segment of third leg, anterior **D** coxa and basis of fourth leg, anterior **E** third endopodal segment of fourth leg, anterior **F** fifth leg, dissected and flattened, anterior. Arrowheads indicate morphological characters different from those in *S. pubescens* Chislenko, 1978.

Fourth leg (Figs 8A, 12D, E) as in *S. pubescens*, except distomedial basal process larger (arrowed in Fig. 12D), both inner setae on third endopodal segment with additional short pinnules (arrowed in Fig. 12E), and inner apical seta on third endopodal segment with short outer pinnules (arrowed in Fig. 12E).

Fifth leg (Figs 8D, 12F) segmentation, general shape, number of armature elements, and most ornamentation as in *S. pubescens*, except exopod proportionately shorter (arrowed in Fig. 8D), second endopodal seta from inner side shorter (arrowed in Fig. 12F), second and third endopodal seta from inner side shorter (both arrowed in Fig. 12F), and spaces between central endopodal seta and two neighbouring setae significantly wider (both arrowed in Fig. 12F). Distal whip on second endopodal seta much shorter than in *S. pubescens*, only about 0.35 times as long as proximal stout part of seta (including transverse serrate comb). Length ratio of endopodal setae, starting from inner side, 1 : 0.4 : 0.6 : 0.5 : 0.4. Length ratio of exopodal setae, starting from inner side, 1 : 0.5 : 0.7 : 0.5 : 0.5 : 0.6.

Sixth leg (Fig. 10B) as in *S. pubescens*.

Variability. Most morphological features in the examined Korean specimens were extremely conservative, including the sensilla and pores pattern on somites, and length ratio of different armature on appendages. Except for the body length, the only other variable feature in the Korean population was the number of spinules on the inner margin of the fifth leg exopod (compare Figs 8D and 12F). We redescribe this species in order to show some previously unreported characters, so they can be compared with those of *Stenhelia pubescens*. Differences from the original description of Mu and Huys (2002) are given in the Discussion section below.

Molecular results

DNA was extracted and the mtCOI fragment successfully PCR-amplified from 23 *Stenhelia* copepod specimens (Table 2), belonging to eight different morpho-species. All the sequences were translated into protein using MEGA and were shown to have no evidence of stop codons, ambiguities or insertions–deletions indicative of non-functional copies of mtCOI. BLAST analyses of GenBank revealed that the obtained sequences are copepod in origin and not contaminants, and one of the GenBank COI sequences (JQ390578.1) from the species *Schizopera leptafurca* Karanovic & Cooper, 2012 was included in our phylogenetic analyses.

Average pairwise distances between morpho-species were found to be very high, with the lowest divergence (7.1%) between the Korean *Itostenhelia polyhymnia* Karanovic & Kim, 2014 and the Russian *Itostenhelia golikovi* (Chislenko, 1978) (Table 3). Second (10.1%) and third (16.9%) lowest divergences were found between *Stenhelia taiae* and *Stenhelia pubescens* and between *Stenhelia taiae* and *Willenstenhelia thalia* Karanovic & Kim, 2014, while those between all other taxa were in excess of 17%. These high divergence values are generally indicative of distinct species by comparison with other crustaceans (Lefébure et al. 2006) and other harpacticoid copepods (Karanovic and

Table 3. Average pairwise maximum likelihood distances (TN model) among mtCOI sequences between each morpho-species (lower diagonal) and within morpho-species (diagonal).

Species	1	2	3	4	5	6	7	8	9
1. <i>Wellstenhelia calliope</i>	-								
2. <i>Itostenhelia polyhymnia</i>	0.271	0.000							
3. <i>Wellstenhelia qingdaoensis</i>	0.267	0.228	-						
4. <i>Wellstenhelia clio</i>	0.202	0.328	0.245	-					
5. <i>Itostenhelia golikovi</i>	0.218	0.071	0.278	0.267	0.006				
6. <i>Willenstenhelia thalia</i>	0.285	0.201	0.291	0.338	0.181	0.008			
7. <i>Schizopera leptafurca</i>	0.302	0.241	0.376	0.344	0.270	0.199	-		
8. <i>Stenhelia taiae</i>	0.317	0.193	0.342	0.240	0.170	0.169	0.245	0.000	
9. <i>Stenhelia pubescens</i>	0.318	0.220	0.352	0.311	0.201	0.173	0.311	0.101	0.000

Cooper 2011a, 2012). Average pairwise distances among the four stenheliin genera were between 17% and 33.8%, indicating only a remote relationship, and are comparable to those among some well accepted canthocamptid and parastenocaridid genera (Karanovic and Cooper 2011a, b). They were certainly comparable to those between *Schizopera leptafurca* and the four stenheliid genera (from 19.9% to 37.6%), although the former belongs to a different subfamily of miraciid harpacticoids.

The highest divergences within morpho-taxa were those between eight specimens of *Willenstenhelia thalia* (0.8%), which all came from the same sampling station (St. 10), although collected on two separate occasions. Divergences between five specimens of *Itostenhelia golikovi* were about 0.6%. (Table 3). These are all indicative of intraspecific variability (Lefébure et al. 2006). Sequences of all other species where we had more than one specimen showed zero divergence, although being of different length (Table 2). The L-form of *Itostenhelia polyhymnia* shows no molecular divergence from the normal form of this species, despite their morphological difference in size and some cuticular ornamentation, although the amplified fragment was very short (Table 2).

All analyses (Fig. 13) supported the presence of at least nine highly divergent lineages and all five of the multisample lineages were supported with high bootstrap values (>74% for ML). The tree topology in our NJ analysis was the same as in the ML analysis (Fig. 13), except the bootstrap values were generally slightly higher. Our MP analysis resulted in two equally parsimonious trees, each 61 steps long, and their consensus also had a very similar topology to our ML tree, except that bootstrap values were generally slightly lower; also the terminal clade in *Willenstenhelia thalia* was not supported in our MP analysis, nor was the sister relationship between *Wellstenhelia calliope* Karanovic & Kim, 2014 and *Wellstenhelia clio* Karanovic & Kim, 2014 (instead a sister relationship was suggested between *Wellstenhelia qingdaoensis* (Ma & Li, 2011) and *Wellstenhelia clio*, but the bootstrap value for this clade was only 39%). Our previous morphological analyses (see Karanovic and Kim 2014) suggested that *Wellstenhelia clio* is more closely related to *Wellstenhelia calliope* than to *Wellstenhelia qingdaoensis* (see above), which is why we have more confidence in our ML analysis than in our MP analysis, and all further molecular results and subsequent discussion will refer to the former (Fig. 13).

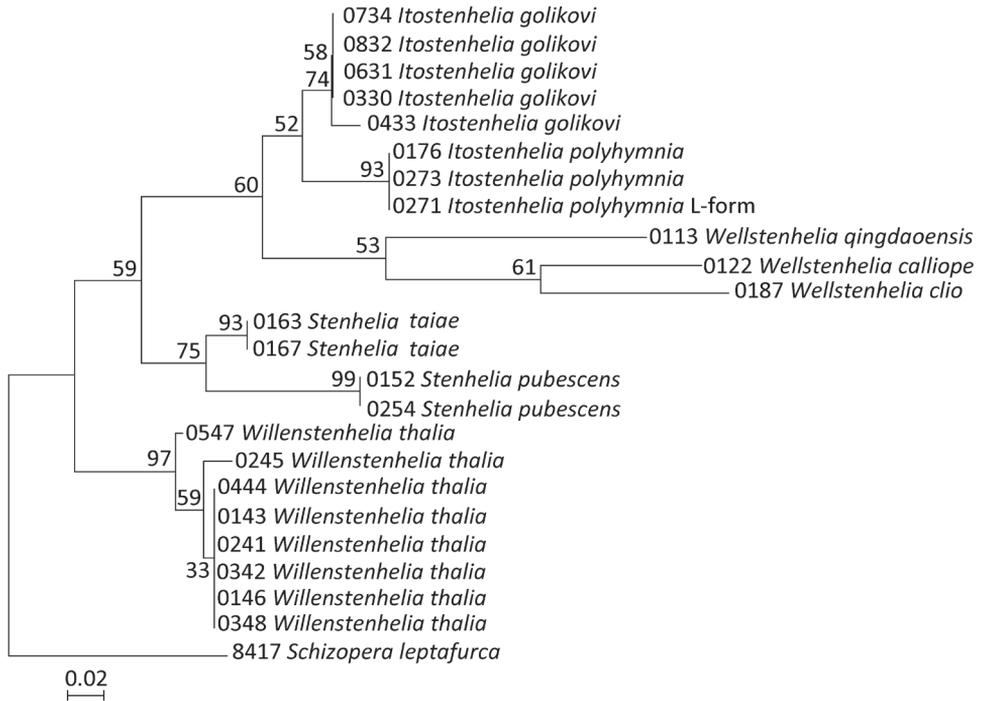


Figure 13. Maximum likelihood (ML) tree based on mtCOI sequence data of 23 stenheliin specimens from Gwangyang Bay (South Korea) and Posyet Bay (Russia), constructed using MEGA v 5.0.3 and an HKY+G model of evolution, with numbers on the branches representing bootstrap values from 500 pseudoreplicates. The tree is rooted with *Schizopera leptafurca* Karanovic & Cooper, 2012 from Western Australia. The cladogram is drawn to scale and the specimen codes correspond to those in Table 2.

All basal nodes are supported only by moderate bootstrap values (between 52% and 75%), which could be explained by the low phylogenetic resolution of the mtCOI gene in basal nodes of the trees, possibly due to saturation at third codon positions (Karanovic and Cooper 2012) and also by various lengths of the fragments amplified (see Table 2). Nevertheless, all four stenheliin genera were well defined. A sister group relationship of *Itostenhelia golikovi* and *Itostenhelia polyhymnia* has the lowest support (52%), yet these two morpho-species are only distinguishable by several settled morphological features, and so different from any other stenheliin analysed here that there is no doubt about their sister-species relationship (see Karanovic and Kim 2014). Another moderately supported lineage is that uniting the three *Wellstenhelia* species (53%), but it was recovered in all analyses despite each species being represented with a single sequence (Table 2); divergences between morpho-species are much higher than in the genus *Itostenhelia*, which is in complete accordance with previously observed morphological evidence. There is also a strongly supported sister group relationship of *Stenhelia pubescens* and *Stenhelia taiae* (bootstrap support 75%). Genera *Itostenhelia* and *Wellstenhelia* form a moderately supported clade (60%), with a similar level of

support suggested for the lineage formed by these two genera and the genus *Stenhelia*. All our analyses showed *Willenstenhelia* as a sister group to all other stenheliins, suggesting only a remote relationship; although this was not apparent from the divergence values (Table 3), it is strongly supported by the previously studied morphological data (see Karanovic and Kim 2014).

Discussion

Phylogenetic implications. Our phylogenetic analysis (Fig. 13) resulted in demonstrating a polyphyly of the genus *Delavalia* Brady, 1869, as postulated by Mu and Huys (2002), because all species described or redescribed in this paper would traditionally be (and *Wellstenhelia qingdaoensis* and *Itostenhelia golikovi* indeed used to be) classified as belonging to this genus. However, the position of the genus *Stenhelia* deep inside this stenheliin group suggests that the two-segmented endopod of the first leg must have originated independently at least in *Willenstenhelia* and *Itostenhelia* /*Wellstenhelia*. The simplicity of the genus-group division based on this morphological character alone was recently demonstrated in the closely related subfamily Diosaccinae Sars, 1906 by Karanovic and Cooper (2012), also based on the combined molecular and morphological approach. A more robust phylogeny of miraciids in general and stenheliins in particular would have to be based on a wider taxon sampling and more genes (including some slower evolving nuclear ones, such as 18S; see Karanovic and Krajcicek 2012a), but the initial congruent data between morphology and genes (Karanovic and Kim 2014) are encouraging for this group of harpacticoid copepods with very few species being resampled after their initial description and many with even their types lost. Also encouraging was the fact that the topology of our trees changed very little depending on the method used (with essentially no difference between NJ and ML analyses), which may suggest that our data are robust (i.e. phylogenetically informative), despite a relatively short segment of the mtCOI gene being amplified (especially in some specimens; see Table 2).

The smallest average divergence values in mtCOI gene (Table 3) were observed between two allopatric (Korea/Russia) species pairs: *Itostenhelia polyhymnia* /*Itostenhelia golikovi* and *Stenhelia taiiae* /*Stenhelia pubescens* (7.1% and 10.1% respectively). Average divergence values between all sympatric Korean stenheliins were very high (all in excess of 16.9%), which suggests a long independent evolutionary history. This is also reflected in their numerous morphological differences (Karanovic and Kim 2014). To us this suggests a potential for niche partitioning with minimal competition for resources, and is very similar to some recently observed examples of sympatric Australian diosaccins (Karanovic and Cooper 2012). It means that multiple colonisations are a better model for explaining this unprecedented diversity in a small Korean bay than is an explosive radiation, despite the fact that surrounding areas do not hold a high diversity currently. However, without any fossil record we can only guess what the diversity of this group in East Asia was historically. Anthropogenic translocation may

also be a contributing factor, as for some other copepod groups (see Karanovic and Krajicek 2012a), and especially through ships' ballast water discharge (Reid and Pinto-Coelho 1994; Lee 1999) or ship's hull biofouling. However, this is just a speculation at this stage, but the presence of *Willenstenhelia minuta* (A. Scott, 1902) in the Suez Canal in Egypt (Gurney 1927) is a sign that these animals are easily dispersed even in artificial habitats.

Micro-characters in harpacticoid taxonomy. Lang (1965) was the first to start paying special attention to somite ornamentation in harpacticoids, and to use it as a diagnostic character in species descriptions and delineations, especially in regard to the spinules pattern on urosomites. Pores and sensilla pattern have not been used in harpacticoid taxonomy until recently, despite their usefulness being demonstrated in distinguishing closely related species of both calanoid (Fleminger 1973; Mauchline 1977; Malt 1983; Koomen 1992) and cyclopoid copepods (Strickler 1975; Baribwegure and Dumont 1999; Baribwegure et al. 2001; Baribwegure and Mirabdullayev 2003; Alekseev et al. 2006; Karanovic and Krajicek 2012a; Karanovic et al. 2012). Initial studies in harpacticoids showed different results in different groups. In the freshwater family Parastenocarididae Chappuis, 1940 a combined morphological and molecular approach showed that spinules ornamentation on urosomites can be used to distinguish between closely related sister species (Karanovic and Cooper 2011a); however, sensilla pattern seems to be extremely conservative within certain lineages (Karanovic and Cooper 2011a; Karanovic et al. 2012; Karanovic and Lee 2012), thus being potentially useful in reconstructing their phylogenetic relationships. Several examined species of the parastenocaridid genus *Proserpinicaris* Jakobi, 1972 all have 45 pairs of sensilla on their body (Karanovic et al. 2012), while those of the genus *Parastenocaris* Kessler, 1913 have only 40 pairs of sensilla (Karanovic and Lee 2012). Their homologisation seems to be relatively uncomplicated, and may prove useful in future revisions of this problematic family. In the family Ameiridae Monard, 1927, a study of several marine species showed a greater diversity in the sensilla and pores pattern even between closely related species (Karanovic and Lee 2012), suggesting them as very useful characters for species delineation. Predictably, their homologisation proved to be much more difficult. Large differences in the sensilla and pores pattern were observed between the stenheliin genera *Itostenhelia*, *Wellstenhelia* and *Willenstenhelia*, but very few between closely related species and with almost non-existent intraspecific variability (Karanovic and Kim 2014).

In this study, one of our aims was to examine pores and sensilla pattern of the two closely related *Stenhelia* congeners. Differences involved not just relative positions of some pores and sensilla, but also a complete absence of some. Cephalothoracic shield has one sensilla pair less and one pore pair more in *S. taiiae* than in *S. pubescens* (compare Figs 1B and 8B). Genital double-somite in *S. taiiae* has the ventral posterior pair of sensilla less widely spaced and the dorsalmost anterior pair of sensilla more widely spaced than in *S. pubescens* (compare Figs 3A, B and 10A, B). Finally, the anal somite in *S. pubescens* lacks the dorsal pair of pores (compare Figs 3A and 10A). Differences between these two species in the cuticular pores and sensilla pattern are no fewer than

differences in the more traditionally used macro-morphological characters, such as the length of caudal rami (compare Figs 3A and 10A), shape and armature proportions of the fifth leg (Figs 7B and 12F), several differences in shape and ornamentation of the swimming legs (Figs 5D, 6B, 7A and 12A, C, D, E), and spinular ornamentation of the urosomites (Figs 1D, E and 8D, E). This is all very surprising given their relatively low divergence values in the mtCOI gene of only 10.1% (see Table 3).

Almost all pores and sensilla can be homologised in these two species without many problems, suggesting a potential use of these structures in future phylogenetic reconstructions of harpacticoid copepods. However, many more families would have to be studied before this could happen. Even so, these preliminary studies in three of the four largest harpacticoid families (Boxshall and Halsey 2004) suggest that these characters hold a huge potential for phylogenetic studies, especially where traditional macro-morphological characters are extremely conservative (family Parastenocarididae, for example) or where they show a great number of homoplastic changes (in most subterranean taxa; see Karanovic and Hancock 2009; Karanovic 2010).

Discrepancies between original descriptions and redescrptions. Careful examination of our topotypes of *Stenbelia pubescens* revealed a number of morphological differences from the original description by Chislenko (1978). We did not examine the types deposited at the Zoological Museum in St. Petersburg, because they are in bad condition, as are most specimens deposited there by Chislenko (pers. comm. Dr Elena Chertoprud, Moscow State University). We were able to check this for the holotype of *Enhydrosoma intermedia* Chislenko, 1978 for example (see Kim et al. in press). Most importantly, we confirm that the second innermost seta on the fifth leg endopod is transformed (see Fig. 3F), with a characteristic transverse posterior serrate comb near mid-length. This was inconclusive in the original description, and it is one of the major synapomorphies of the genus *Stenbelia* as redefined by Mu and Huys (2002). Other major differences between the original description and our redescription include the number of setae on the antennula, antenna, and maxilliped, and it is more probable that they are observational errors on Chislenko's part than intraspecific variability. For example, his drawings show only 6.8.2.3.3 setae on the second to sixth antennular segments, while in reality that formula is 11.9.6.3.4 (see Figs 2B, 5A). Similarly, he probably overlooked two very slender setae on the ultimate endopodal segment of antenna (Fig. 5B) and one on the second endopodal segment of maxilliped (Fig. 4F). The latter is present in most stenheliins that have been studied in detail. Expectedly, there are numerous other smaller differences in the ornamentation of somites and appendages, just because they were not studied in detail or not studied at all by Chislenko (for example, intercoxal sclerites of the swimming legs, sensilla and pore pattern of most somites, etc.). Two other smaller differences are worth mentioning: long setules on the caudal rami armature and a curved seta on the third exopodal segment of the fourth leg. The former are limited to distal tips of the innermost apical and longest lateral caudal setae (Figs 2G, 3A, B), and are not present along the entire length of the armature elements as illustrated by Chislenko (1978, p. 194, fig. 9.2). It is possible that he interpreted some filamentous bacterial colonies as long setules, as these can be seen in several places on our

specimens (see Fig 1C). He has similarly mistaken a bacterial filamentous growth for a slender seta on the maxilliped in his description on *Enhydrosoma intermedia* (see Kim et al. in press). The curved seta on the fourth leg exopod (Fig. 7A) could have been interpreted as a mounting artefact by Chislenko (1978), who drew this element as all other exopodal setae. Differences between specimens that we examined and those examined by Chislenko in the shape of urosome and proportions of the genital double-somite are clearly a consequence of different compression during mounting. We do not think any of the above mentioned differences could be attributed to intraspecific variability, as we examined topotypes and found very little variability among errors. In all our samples from the Russian Far East *Stenhelia pubescens* and *Itostenhelia golikovi* were the only two stenheliins, so there is no possibility that the topotypes we redescribed here belong to a different species than specimens described by Chislenko (1978).

As for the differences between Korean and Chinese populations of *Stenhelia taiae*, they are all minor and some could possibly be contributed to geographic intraspecific variability. We did not examine the types of this species either, but the original drawings of Mu and Huys (2002) are recent, very skilful and detailed, and most differences involve minute details of ornamentation of somites. For example, we could not verify the presence of ventrolateral pores on the genital double-somite and on the third urosomite, despite making high resolution SEM photographs of this area (see Fig. 8D, E). Similarly, Mu and Huys (2002) reported two anterior lateral sensilla on the cephalothoracic shield, as in *Stenhelia pubescens* (see Fig. 1B), but we could only observe one sensilla in that spot (arrowed in Fig. 8B). It is more plausible that these difference are a result of intraspecific variability than of observational errors, as most other sensilla and pores are in exactly the same spot, including closely spaced ventral posterior sensilla on the genital double-somite, ventral pores on the anal somite, and tubular pore on the posterior ventral margin of the caudal ramus (Fig. 10B, C). It is, however, quite certain that Mu and Huys (2002) overlooked several lateral sensilla and pores on the cephalothoracic shield, especially along the ventral margin, as these are present in all harpacticoids examined in detail so far, and in all stenheliins examined here and elsewhere (see Karanovic and Kim 2014). Unfortunately, some of them are actually only visible from ventral side in some taxa (see Fig. 2), and sometimes filamentous bacteria and other epiphytes can be mistaken for sensilla (compare, for example, our Figs 1C and 8C).

Morphology and phylogeny of *Stenhelia*. Major synapomorphy of the eight species currently recognised as members of this genus, as redefined by Mu and Huys (2002), is the transformed second innermost seta on the female fifth leg endopod. The condition of this character was unknown in *Stenhelia pubescens* before our redescription, but we confirm its presence above (see Figs 3F, 7B). Monophyly of this genus has also been supported in our molecular analyses (Fig. 13). Mu and Huys (2002) recognised two major groups of species in the genus based on the number of setae on the third endopodal segment of the third leg. The first group includes the type species *Stenhelia gibba* and two other congeners: *S. curviseta* and *S. proxima*. They all have two inner setae on that segment, and are distributed in the Northern Atlantic and the Mediterranean Sea (Lang 1948; Apostolov and Marinov 1988), but differ markedly in

the length ratio of armature elements on the fifth leg, as well as in the relative length of the first endopodal segment of the first leg. The other group has three inner setae on the third endopodal segment of the third leg and contains one species from the Atlantic Ocean (*S. divergens*) and four from the Northern Pacific (*S. peniculata*, *S. pubescens*, *S. sheni*, and *S. taiiae*). Mu and Huys (2002) noticed that the only Atlantic species in the second group can be distinguished from its Pacific congeners by the shape of the first leg endopod, and they also provided a useful key to species. It should be noted that the second group of species is based on a plesiomorphic character state and that the condition of this character in the first group could be homoplastic. It is quite possible that one of three inner setae can be reduced convergently, and it does not even have to be the same seta to produce the apparent two-inner-setae condition (for some examples of this see Karanovic and Hancock 2009; Karanovic et al. 2013). Morphology, however, did suggest that the three East Asian species are quite similar in comparison to other congeners (Mu and Huys 2002), and testing that hypothesis was one of major aims of our study. Our reconstructed molecular phylogeny (Fig. 13) confirmed this hypothesis at least for two East Asian species, with remarkably low divergence values (Table 3) between *S. pubescens* and *S. taiiae* specimens. The divergence value of 10.1% in the mtCOI gene is low not only in comparison with other crustaceans (see Lefébure et al. 2006) but also in comparison with sister-species with parapatric distribution and niche partitioning from the closely related subfamily Diosaccinae (see Karanovic and Cooper 2012), where these values were in excess of 15%. Even lower divergence rates were observed between two sister species of the genus *Itostenhelia* (see Karanovic and Kim 2014), which may imply that either this gene evolves more slowly in stenheliins or that the rate of speciation is higher. Similarly low divergence rates were found recently between several Western Australian species of the parastenocaridid genus *Kinnecaris* Jakobi, 1972 (see Karanovic and Cooper 2011a), which are all short range endemics and allopatric in distribution, with only minute morphological differences, and thus probably a product of a relatively recent speciation. *Stenhelia pubescens* and *S. taiiae* are also allopatric species, of course, but their numerous morphological differences stand in stark contrast to their low divergence rates in the mtCOI gene.

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Two new species of Trichoceridae from the Middle Jurassic Jiulongshan Formation of Inner Mongolia, China

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Abstract

Two new species, *Eotrichocera* (*Archaeotrichocera*) *longensis* **sp. n.** and *Eotrichocera* (*Archaeotrichocera*) *amabilis* **sp. n.** of Trichoceridae are described based on a combination of the following characters: Sc ending proximad of the forking of R₂, shape of d cell and A₂ rather short and bending sharply toward posterior margin. These fossil specimens were collected from the Middle Jurassic Jiulongshan Formation of Daohugou in Inner Mongolia, China.

Keywords

Diptera, *Eotrichocera*, *Archaeotrichocera*, Fossil, Daohugou

Introduction

Trichoceridae is a family of medium-sized dipterans, commonly called winter crane flies, Yang and Yang (1995) found that just a few adults can live in cold environment, even in winter, and indicated that the name of winter crane flies might not be proper. However, the adults (include the largest species of *Trichocera*) not only live in cold environment, but also mate and lay eggs under the snow cover in winter (Hågvar and Krzemińska 2007). Hence, the common name of winter crane flies is proper. The adults live in damp places close to lakes, rivers, or streams and most of them feed on plant fluids (Yang 2009); while the larvae live in moist or wet or terrestrial biotopes and feed on plant debris, decaying leaves in forests, mushrooms and animal droppings (Dahl and Alexander 1976) or take cankered plants or animal bodies as food (Yang 2009).

There are 77 species of fossil and amber trichocerids, which have been assigned into three subfamilies: Trichocerinae, Paracladurinae and Kovalevinae; and twelve genera: *Cladoneura* Scudder, 1894; *Eotrichocera* Kalugina, 1985; *Rasnitsynina* Krzemińska, Krzemiński & Dahl, 2009; *Mailotrichocera* Kalugina, 1985; *Paleotrichocera* Kalugina, 1986; *Karatina* Krzemińska, Krzemiński, Dahl & Lukashevich, 2009; *Trichocera* Meigen, 1803; *Tanyochoreta* Zhang, 2006; *Zherikhinina* Krzemińska, Krzemiński & Dahl, 2009; *Undaya* Krzemińska, Krzemiński & Dahl, 2009; *Kovaleva* Krzemińska, Krzemiński & Dahl, 2009; *Paracladura* Brunetti, 1911 (Krzemińska et al. 2009a). The oldest species of trichocerids, *Mailotrichocera variabilis*, *M. mikereichi* and *M. zessini* have been described from Lower Jurassic of Germany (Krzemińska et al. 2009a).

Among them, there are eight species in three genera described from the Daohugou locality of China: *Eotrichocera* (*Archaeotrichocera*) *ephemera* Zhang, 2006; *Tanyochoreta integra* Zhang, 2006; *Tanyochoreta chifengica* Zhang, 2006; *Tanyochoreta* (*Sinotrichocera*) *parva* Zhang, 2006; *Eotrichocera* (*Archaeotrichocera*) *conica* Krzemińska, Krzemiński & Ren, 2009; *Eotrichocera* (*Archaeotrichocera*) *rara* Krzemińska, Krzemiński & Ren, 2009; *Eotrichocera* (*Archaeotrichocera*) *spatiosa* Liu, Shih & Ren, 2012 and *Zherikhinina reni* Krzemińska, Krzemiński & Dahl, 2009.

Furthermore, *Sinotrichocera* Zhang, 2006 has been changed as a subgenus belonging to *Tanyochoreta*; *Oligotrichocera* Dahl, 1971 as a subgenus belonging to *Trichocera* Podenas, 2001; *Trichonomites* Kalugina, 1986 and *Paleotrichocera* Kalugina, 1986 are synonymized (Krzemińska et al. 2009a). All genera and species of Trichoceridae Kertész, 1902, after revisions and transfers, are summarized in Table 1, which is updated and expanded from the Tables 1 and 4 in Krzemińska et al. 2009a.

The specimens for this study were collected from the Jiulongshan Formation of the Daohugou Village in Inner Mongolia, China. The Daohugou fossil-bearing beds are considered as the late Middle Jurassic (Bathonian-Callovian boundary, 165 Mya) (Ren et al. 2002; Gao and Ren 2006; Ren et al. 2010a; Shi et al. 2011). Daohugou is one of the localities where the fossils of Yanliao biota were distributed. A huge number of fossil insects have been reported (Ren and Engel 2007; Engel and Ren 2008; Liu and Ren 2008; Ren et al. 2009; Wang and Ren 2009; Gu et al. 2010; Ren et al. 2010b; Wang et al. 2010; Wang et al. 2012; Yang et al. 2012).

Table 1. Fossil species of Trichoceridae Kertész, 1902.

Genus	Species	Author(s)	Date	Age	Locality
<i>Cladoneura</i>	<i>C. willistoni</i>	Scudder	1894	Lower Oligocene	Florissant, USA
<i>Eotrichocera</i> (<i>Archaeotrichocera</i>)	<i>E. (A.) ephemera</i>	Zhang	2006	Middle Jurassic	Daohugou, China
	<i>E. (A.) conica</i>	Krzemińska, Krzemiński & Ren	2009a	Middle Jurassic	Daohugou, China
	<i>E. (A.) rara</i>	Krzemińska, Krzemiński & Ren	2009a	Lower Cretaceous	Kempendyay, Russia
	<i>E. (A.) spatiosa</i>	Liu, Shih & Ren	2012a	Middle Jurassic	Daohugou, China
<i>Eotrichocera</i> (<i>Eotrichocera</i>)	<i>E. (E.) christinae</i>	Kalugina	1985	Lower Jurassic or earlier Middle Jurassic	Novospasskoe, Russia
<i>Karatina</i>	<i>K. longipes</i>	Rohdendorf	1964	Upper Jurassic	Karatau, Kazakhstan
	<i>K. explorans</i>	Krzemińska, Krzemiński, Dahl & Lukashevich	2009a	Lower Cretaceous	Baissa, Russia
	<i>K. pellita</i>	Krzemińska, Krzemiński, Dahl & Lukashevich	2009a	Upper Jurassic	Karatau, Kazakhstan
<i>Kovaleva</i> (<i>Kovaleva</i>)	<i>K. (K.) fragmentosa</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Unda and Daya, E. Transbaikalia
	<i>K. (K.) hirsuta</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Daya, E. Transbaikalia
	<i>K. (K.) obscura</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Daya, Unda and Shevia, E. Transbaikalia
	<i>K. (K.) sheviae</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Shevia, E. Transbaikalia
	<i>K. (K.) volodii</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Daya, E. Transbaikalia
<i>Kovaleva</i> (<i>Vladimirevna</i>)	<i>K. (V.) mirabilis</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Daya, E. Transbaikalia
<i>Mailotrichocera</i>	<i>M. jurassica</i>	Kalugina	1985	Uppermost middle or earliest Upper Jurassic	Uda, E. Transbaikalia
	<i>M. gracilis</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Daya, Unda and Shevia, E. Transbaikalia
	<i>M. mikereichi</i>	Krzemińska, Krzemiński & Ansoerge	2009a	Lower Jurassic	Dobbertin, Germany; Grimmen, Germany
	<i>M. ovifera</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/ Cretaceous boundary	Unda, E. Transbaikalia
	<i>M. prisca</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Unda and Shevia, E. Transbaikalia
	<i>M. sukachevae</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Unda, E. Transbaikalia
	<i>M. variabilis</i>	Krzemińska, Krzemiński & Ansoerge	2009a	Lower Jurassic	Dobbertin, Germany; Grimmen, Germany
	<i>M. zessini</i>	Krzemińska, Krzemiński & Ansoerge	2009a	Lower Jurassic	Grimmen, Germany
<i>Paleotrichocera</i>	<i>P. mongolica</i>	Kalugina	1986	Lower Cretaceous	Gurvan Erenyi Nuru, Mongolia
<i>Paracladura</i>	<i>P. caucasiana</i>	Krzemińska, Krzemiński & Dahl	2009a	Middle Miocene	Stavropol, Caucasus

Genus	Species	Author(s)	Date	Age	Locality
<i>Rasnitsynina</i>	<i>R. collecta</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Shevia, E. Transbaikalia
	<i>R. minae</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Shevia and Daya, E Transbaikalia
<i>Tanyochoreta</i> (<i>Sinotrichocera</i>)	<i>T. (S.) parva</i>	Zhang	2006	Middle Jurassic	Daohugou, China
<i>Tanyochoreta</i> (<i>Tanyochoreta</i>)	<i>T. (T.) chifengica</i>	Zhang	2006	Middle Jurassic	Daohugou, China
	<i>T. (T.) integra</i>	Zhang	2006	Middle Jurassic	Daohugou, China
<i>Tanyochoreta</i> (<i>Trichokana</i>)	<i>T. (T.) composita</i>	Krzemińska, Krzemiński & Dahl	2009a	Upper Jurassic	Karatau, Kazakhstan
	<i>T. (T.) fracta</i>	Krzemińska, Krzemiński & Dahl	2009a	Upper Jurassic	Karatau, Kazakhstan
	<i>T. (T.) minuta</i>	Krzemińska, Krzemiński & Dahl	2009a	Upper Jurassic	Karatau, Kazakhstan
	<i>T. (T.) tenuis</i>	Krzemińska, Krzemiński & Dahl	2009a	Upper Jurassic	Karatau, Kazakhstan
	<i>T. (T.) zagadka</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Unda, E Transbaikalia
	<i>T. (T.) zbulwami</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Daya and Unda, E Transbaikalia
<i>Trichocera</i>	<i>T. scudleri</i>	Meunier	1915	Upper Oligocene	Rott, Germany
	<i>T. miocaenica</i>	Statz	1934	Upper Oligocene	Rott, Germany
	<i>T. antiqua</i>	Dahl	1971	Upper Eocene	Baltic
	<i>T. primaeva</i>	Dahl	1971	Upper Eocene	Baltic
	<i>T. fujiyamai</i>	Gentilini	1984	Upper Miocene	Monte Castellaro, Italy
	<i>T. anbar</i>	Podenas	2001	Upper Eocene	Baltic
	<i>T. bona</i>	Podenas	2001	Upper Eocene	Baltic
	<i>T. cerea</i>	Podenas	2001	Upper Eocene	Baltic
	<i>T. diluta</i>	Podenas	2001	Upper Eocene	Baltic
	<i>T. ebenos</i>	Podenas	2001	Upper Eocene	Baltic
	<i>T. christelae</i>	Krzemińska, Krzemiński & Dahl	2009a	Upper Eocene	Baltic
	<i>T. corami</i>	Krzemińska, Krzemiński & Dahl	2009a	Lower Cretaceous	Purbeck, UK
	<i>T. cretacea</i>	Krzemińska, Krzemiński & Dahl	2009a	Lower Cretaceous	Baissa, Russia
	<i>T. hanswerneri</i>	Krzemińska, Krzemiński & Dahl	2009a	Upper Eocene	Baltic
	<i>T. turgana</i>	Krzemińska, Krzemiński & Dahl	2009a	earlier Lower Cretaceous	Turga, E. Transbaikalia
<i>Undaya</i>	<i>U. alata</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Unda and Shevia, E. Transbaikalia
	<i>U. comis</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Unda, E. Transbaikalia
	<i>U. gargantuina</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Daya and Unda, E. Transbaikalia
	<i>U. hilara</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Unda and Shevia, E. Transbaikalia
	<i>U. kaluginae</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Daya, E. Transbaikalia
	<i>U. lenae</i>	Krzemińska, Krzemiński & Dahl	2009a	Upper Jurassic	Shar-Teg, Mongolia

Genus	Species	Author(s)	Date	Age	Locality
	<i>U. lukashevichae</i>	Krzemińska, Krzemiński & Dahl	2009a	Upper Jurassic	Shar-Teg, Mongolia
	<i>U. maxima</i>	Krzemińska, Krzemiński & Dahl	2009a	Lower Cretaceous	Kempendyay, Russia
	<i>U. mitis</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Daya and Unda, E. Transbaikalia
	<i>U. molesta</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Unda and Daya, E. Transbaikalia
	<i>U. namdyriensis</i>	Krzemińska, Krzemiński & Dahl	2009a	Lower Cretaceous	Kempendyay, Russia
	<i>U. parvula</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Daya and Unda, E. Transbaikalia
	<i>U. pura</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Unda and Daya, E. Transbaikalia
	<i>U. salsa</i>	Krzemińska, Krzemiński & Dahl	2009a	Lower Cretaceous	Kempendyay, Russia
	<i>U. savina</i>	Krzemińska, Krzemiński & Dahl	2009a	Jurassic/Cretaceous boundary	Savina, E. Transbaikalia
	<i>U. saxea</i>	Krzemińska, Krzemiński & Dahl	2009a	Lower Cretaceous	Kempendyay, Russia
	<i>U. triangula</i>	Krzemińska, Krzemiński & Dahl	2009a	Lower Cretaceous	Kempendyay, Russia
	<i>Z. itatica</i>	Kalugina	1985	Middle Jurassic	Kubekovo, Russia
	<i>Z. alastos</i>	Krzemińska & Lukashevich	2009b	Upper Jurassic	Shar Tëg, Mongolia
	<i>Z. baissana</i>	Krzemińska, Krzemiński & Dahl	2009a	Lower Cretaceous	Baissa, Russia
	<i>Z. bontsagana</i>	Krzemińska, Krzemiński & Dahl	2009a	Lower Cretaceous	Bon Tsagan, Mongolia
<i>Zherikhinina</i>	<i>Z. karatavica</i>	Krzemińska, Krzemiński & Dahl	2009a	Upper Jurassic	Karatau, Kazakhstan
	<i>Z. novospasskaya</i>	Krzemińska, Krzemiński & Dahl	2009a	later Lower or early Middle Jurassic	Novospasskoe, Russia
	<i>Z. reni</i>	Krzemińska, Krzemiński & Dahl	2009a	Middle Jurassic	Daohugou, China
	<i>Z. tola</i>	Krzemińska, Krzemiński & Dahl	2009a	Lower Cretaceous	Onokhoy, Mongolia
	<i>Z. zherikhini</i>	Krzemińska, Krzemiński & Dahl	2009a	Upper Jurassic	Karatau, Kazakhstan

Materials and methods

The wing venation nomenclature used in this paper is based on the interpretations and system proposed by Lukashevich (2004) and Krzemińska et al. (2009a). The fossil specimens were examined under a Leica MZ7.5 dissecting microscope and illustrated with the aid of a drawing tube attachment. Line drawings were prepared with Adobe Photoshop CS3 Extended graphics software.

All specimens studied in the paper are housed in the Key Lab of Insect Evolution and Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China.

Systematic paleontology

Family Trichoceridae Kertész, 1902

Genus *Eotrichocera* Kalugina, 1985

Subgenus *Archaeotrichocera* Krzemińska, Krzemiński & Dahl, 2009

Type species. *Eotrichocera* (*Archaeotrichocera*) *ephemera* Zhang, 2006

Other included species. *Eotrichocera* (*Archaeotrichocera*) *conica* Krzemińska, Krzemiński & Ren, 2009; *Eotrichocera* (*Archaeotrichocera*) *rara* Krzemińska, Krzemiński & Ren, 2009; *Eotrichocera* (*Archaeotrichocera*) *spatiosa* Liu, Shih & Ren, 2012.

Key to the species of *Eotrichocera* (*Archaeotrichocera*)

- | | | |
|---|---|---|
| 1 | Sc ending at anterior margin distad of R_2 | 2 |
| – | Sc ending at anterior margin proximad of R_2 | 3 |
| 2 | Large size (wing length 12.0 mm)..... | |
| | <i>E. (A.) spatiosa</i> Liu, shih & Ren, 2012 (Daohugou, J_2) | |
| – | Medium size (wing length 5.5 mm)..... | |
| | <i>E. (A.) rara</i> Krzemińska, Krzemiński & Ren, 2009 (Daohugou, J_2) | |
| 3 | Crossvein sc-r distad of 1/2 (at 2/3) of length of R_s | 4 |
| – | Crossvein sc-r proximad of or at 1/3 of length of R_s | 5 |
| 4 | R_s forking distad of 2/3 (at 0.77) times of wing length..... | |
| | <i>E. (A.) ephemera</i> Zhang, 2006 (Daohugou, J_2) | |
| – | R_s forking proximad of 2/3 (at about 0.53) times of wing length..... | |
| | <i>E. (A.) longensis</i> sp. n. (Daohugou, J_2) | |
| 5 | A_2 long (0.22 times as long as wing), d cell narrow and long ($W/L=0.43$)..... | |
| | <i>E. (A.) conica</i> Krzemińska, Krzemiński & Ren, 2009 (Daohugou, J_2) | |
| – | A_2 short (0.13 times as long as wing), d cell broad ($W/L=0.58$)..... | |
| | <i>E. (A.) amabilis</i> sp. n. (Daohugou, J_2) | |

Eotrichocera (*Archaeotrichocera*) *longensis* sp. n.

<http://zoobank.org/8A0D358E-7BCA-476B-A0A9-6EECA93FCBA8>

http://species-id.net/wiki/Eotrichocera_longensis

Etymology. “*longensis*” is a Latin word, referring to the long leg of this specimen.

Diagnosis. Sc rather short about 0.65 times as long as the wing and ending at anterior margin proximad of R_2 ; R_s forking proximad of 2/3 (at about 0.55) times of wing length; the d-cell narrow and long (about 2.5 times as long as wide); A_2 short and bending sharply toward anterior margin (angle about 128°).

Holotype. An almost complete female specimen with well-preserved body, wings and head. Specimen number CNU-DIP-NN2013133. Wing length 9.0 mm, width 3.8 mm (Figs 1A, 2, 3A).

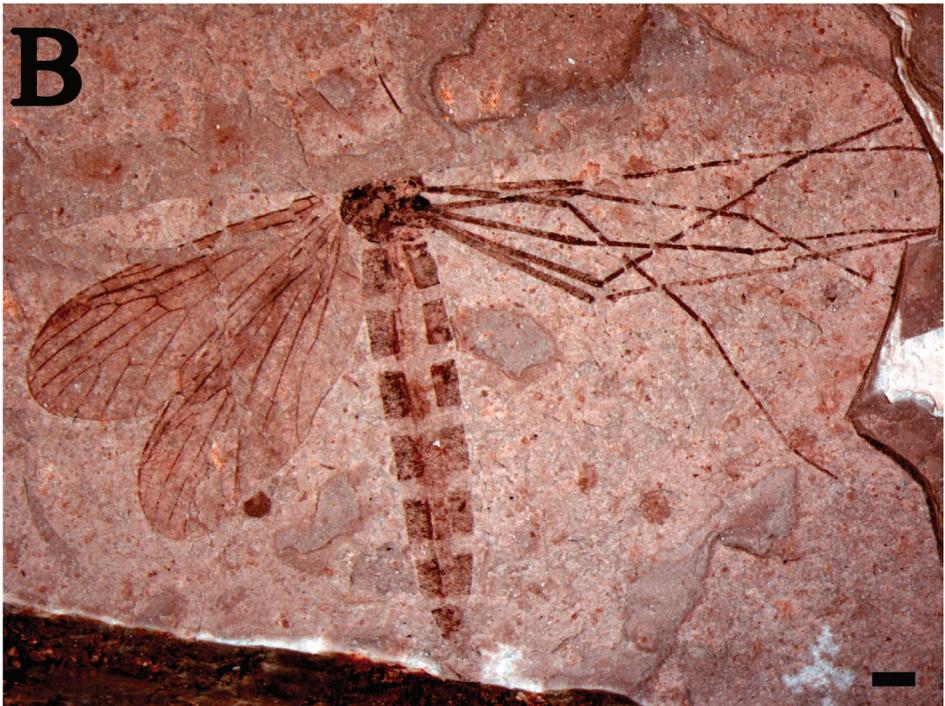


Figure 1. *Eotrichocera (Archaeotrichocera) longensis* sp. n. Holotype, specimen CNU-DIP-NN2013133 **A** Photograph. Paratype, specimen CNU-DIP-NN2013131 **B** Photograph. Scale bars = 1 mm.

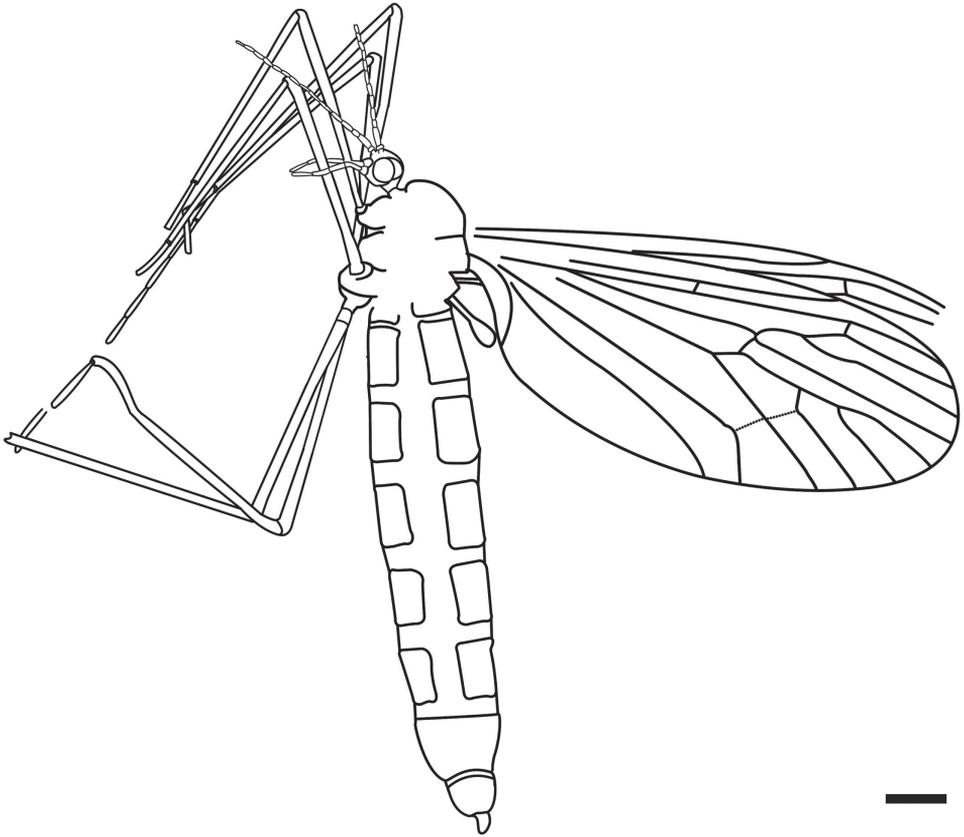
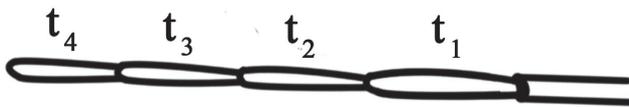
A**B**

Figure 2. *Eotrichocera (Archaeotrichocera) longensis* sp. n. Holotype, specimen CNU-DIP-NN2013133
A Line drawing **B** Tarsus of the mid leg. Scale bars = 1 mm; t_1 = the first segment of tarsus; t_2 = the second segment of tarsus; t_3 = the third segment of tarsus; t_4 = the fourth segment of tarsus.

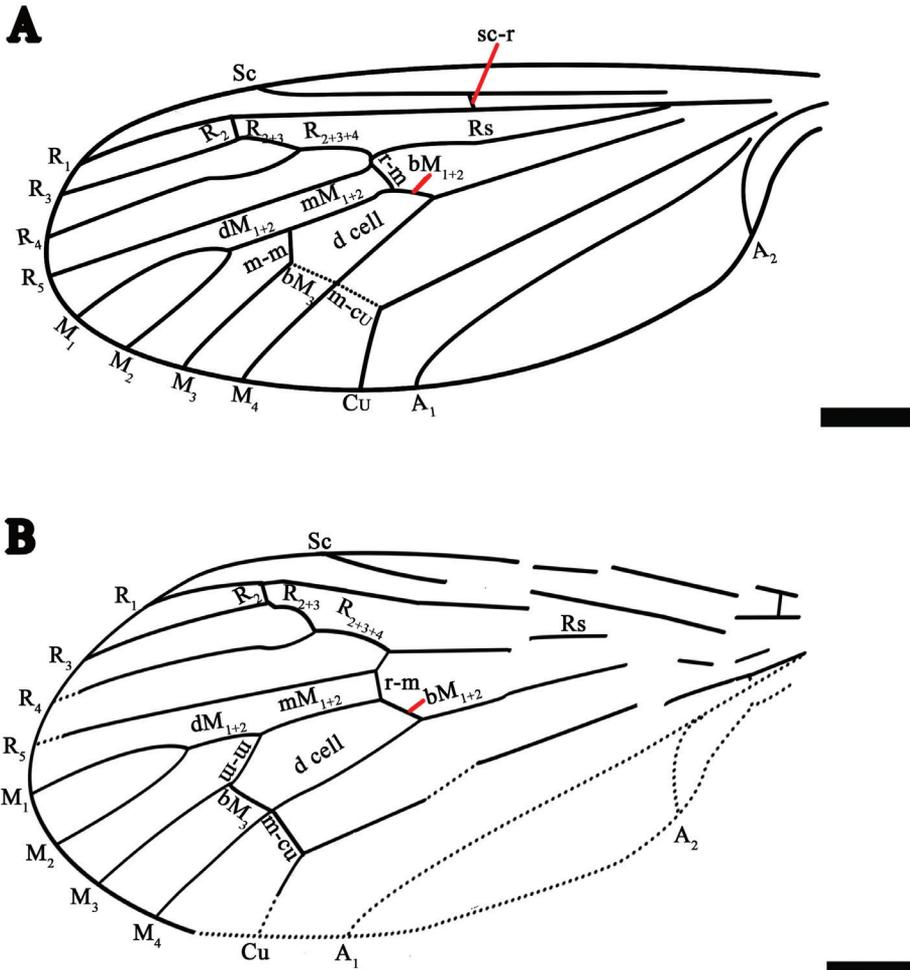


Figure 3. *Eotrichocera (Archaeotrichocera) longensis* sp. n. Holotype, specimen CNU-DIP-NN2013133 **A** Line drawing of left wing. Paratype, specimen CNU-DIP-NN2013131 **B** Line drawing of left wing. Scale bars = 1 mm

Paratype. A female specimen with body and wings, specimen number CNU-DIP-NN2013131. Wing length 7.7 mm, width 3 mm (Figs 1B, 3B).

Locality and horizon. Jiulongshan Formation, Late Middle Jurassic, Daohugou Village, Ningcheng County, Inner Mongolia Autonomous Region, China.

Description. Based on Holotype, different characters of the paratype CNU-DIP-NN2013131 in brackets. Medium-sized winter crane flies, body length (including head) 13 mm with well preserved wings, body and head, [paratype body length (excluding head) 10.5 mm].

Head: Antenna very long, about 3.5 times as long as the head length, palpi about two times as long as the head length, compound eyes preserved.

Table 2. Comparison of key characters among the two new species and other species of *Eotrichocera* (*Archaeotrichocera*) Krzemińska, Krzemiński & Dahl, 2009. L/W = ratio of length/width; W/L = ratio of width/length.

Key characters	<i>E. (A.) ephemera</i> Zhang, 2006	<i>E. (A.) conica</i> Krzemińska, Krzemiński & Ren, 2009	<i>E. (A.) rara</i> Krzemińska, Krzemiński & Ren, 2009	<i>E. (A.) spatiosa</i> Liu, Shih & Ren, 2012	<i>E. (A.) longensis</i> sp. n.	<i>E. (A.) amabilis</i> sp. n.
Wing length, in mm and (L/W)	7.1 (L/W=2.8)	10.0 (L/W=3)	5.5	12.0 (L/ W=2.7)	9.0 (L/W=2.3)	5.2 (L/W=2.2)
Sc length and ending at anterior margin	0.77 times of wing length, ending proximad of R ₂	0.71 times of wing length, ending proximad of R ₂	0.77 times of wing length, ending distad of R ₂	0.84 times of wing length, and ending distad of R ₂	about 0.65 times of wing length, ending proximad of R ₂	about 0.71 times of wing length, ending proximad of R ₂
sc-r position	at 2/3 of length of Rs	at 1/3 of length of Rs	at 1/2 of length of Rs	at 2/3 of length of Rs	at 2/3 of length of Rs	at 1/3 of length of Rs
Position of Rs forking	0.77 times of wing length	0.64 times of wing length	0.57 times of wing length	0.58 times of wing length	0.53 times of wing length	0.55 times of wing length
d-cell W/L (length)	W/L=0.53 (1/6 of wing length)	W/L=0.43 (0.2 times of wing length)	W/L=0.39 (0.21 times of wing length)	W/L=0.47 (0.19 times of wing length)	W/L= 0.4 (almost 1/5 of wing length)	W/L=0.58 (almost 0.17 of wing length)
A ₂ length	long (about 1/4 of wing length), curved evenly to posterior margin	medium (0.22 times of wing length), not reaching posterior margin	rather short (1/5 of wing length) and not reaching posterior margin	short (about 0.21 times of wing length) and curving to posterior margin	short (0.14) times of wing length) and curved to posterior margin	short (0.13) times of wing length) and curved to posterior margin
r-m length	1/5 of length of d-cell	about 1/3 of length of d-cell	1/5 of length of the d-cell	0.24 or 0.15 of length of the d-cell

Thorax: Much higher, in lateral view, than that of the abdomen, subcircular in shape, with robust and well-developed mesonotum. The halteres spoon-type and the length of halteres as long as thorax.

Wings: Wing is shorter than abdomen, not covering the end of the abdomen. Length 9.0 mm [Paratype with wing length of 7.7 mm], narrow and long (about 2.5 times as long as wide); venation clear, Sc rather short about 0.68 times as long as the wing [Paratype Sc rather short, about 0.65 times as long as the wing] and ending at anterior margin proximad of R₂; crossvein sc-r locating at 2/3 of Rs; Rs arising about one-fifth from the base of the wing; R₂₊₃ about 0.8 times as long as R₂₊₃₊₄; R₂ about one-tenth of length of R₃; R₃ almost three times as long as the R₂₊₃; dM₁₊₂ 0.6 times as long as mM₁₊₂, while M₁ 2.5 times of the dM₁₊₂; a well developed m-m crossvein about three-fourth length of bM₃, closing the d-cell and nearly 0.3 length of d-cell; bM₁₊₂ nearly 1.0 times as long as the length of the r-m and the latter at one-fifth of the d-cell; d-cell narrow and long (about 2.5 times as long as wide) and almost one-fifth length of wing; both crossveins m-m and m-cu intersecting with M₄ at the same point; Cu long, curved (angle about 135°) and reaching the wing posterior margin at 0.6 from the base of the wing; the stem of A divided into A₁ and A₂; A₁ long, slightly curving and reaching the wing posterior margin; A₂ short, 0.15 (right wing) [Paratype 0.14] times as long as

wing and almost 0.3 times as long as length of A_1 , bending sharply (angle about 128°) and reaching the wing posterior margin.

Legs: Legs slender and long; the hind leg nearly 1.2 times as long as the abdomen and 1.3 times as long as the wing. Tarsus with five segments; the first segment of tarsus (t_1) is 1.2 times as long as t_2 in mid leg.

Abdomen: Abdomen relatively long and thin, with ten segments. Female genital discernible.

Remarks. *Eotrichocera* (*Archaeotrichocera*) *longensis* sp. n. is assigned to Trichocerinae based on the following characters: d-cell medium, m-cu present; A_2 short, antennae long, flagellomeres thin, much longer than two times of the head length. It belongs to *Eotrichocera* (*Archaeotrichocera*) because of wing length from 7.7 to 9.0 mm and d-cell almost one-fifth of wing length. In addition, it differs from all other known Trichocerinae by its A_2 rather short and bending sharply toward anterior margin (angle about 128°), R_2 relatively long, Sc forking proximad of $2/3$ (at about 0.55) times of wing length, and d-cell narrow and long. To compare the key characters among the new species and other species of *Eotrichocera* (*Archaeotrichocera*), we set up the Table 2.

***Eotrichocera* (*Archaeotrichocera*) *amabilis* sp. n.**

<http://zoobank.org/D32A4E4B-EDF1-4684-802E-92F9617DEAB2>

http://species-id.net/wiki/Eotrichocera_amabilis

Etymology. The specific name of “*amabilis*” is a Latin word, meaning lovely.

Diagnosis. Body small and wing short; Sc 0.71 times as long as wing; the d-cell broad (about 1.7 times as long as wide); A_2 short and bending sharply toward posterior margin (angle about 128°).

Holotype. An almost complete female specimen with well-preserved body, wings and head. Specimen number CNU-DIP-NN2013134, Wing length 5.2 mm, width 2.2 mm (Figs 4A–D, 5A, 6).

Paratype. A specimen with body and wings with partial venation, specimen number CNU-DIP-NN2013132, (Figs 4E, 5B).

Locality and horizon. Jiulongshan Formation, Late Middle Jurassic, Daohugou Village, Ningcheng County, Inner Mongolia Autonomous Region, China.

Description. Based on Holotype, different characters of the paratype CNU-DIP-NN2013132 in brackets. Medium-sized winter crane flies, head length 0.47 mm, body length (including head) 5.8 mm with well preserved body and wings. [Paratype with partial body and wings with partial venation].

Head: antenna very long, about 5.7 times as long as the head length, palpi about two times as long as the head length, compound eyes preserved (Figs 4C, 6).

Thorax: Much higher, in lateral view, than that of the abdomen, subcircular in shape, with robust and well-developed mesonotum.

Wings: Wing is shorter than abdomen, not covering the end of the abdomen. Wing length of 5.2 mm [Paratype with wing length 5.0 mm], narrow and long ($L/W=2.2$); ve-

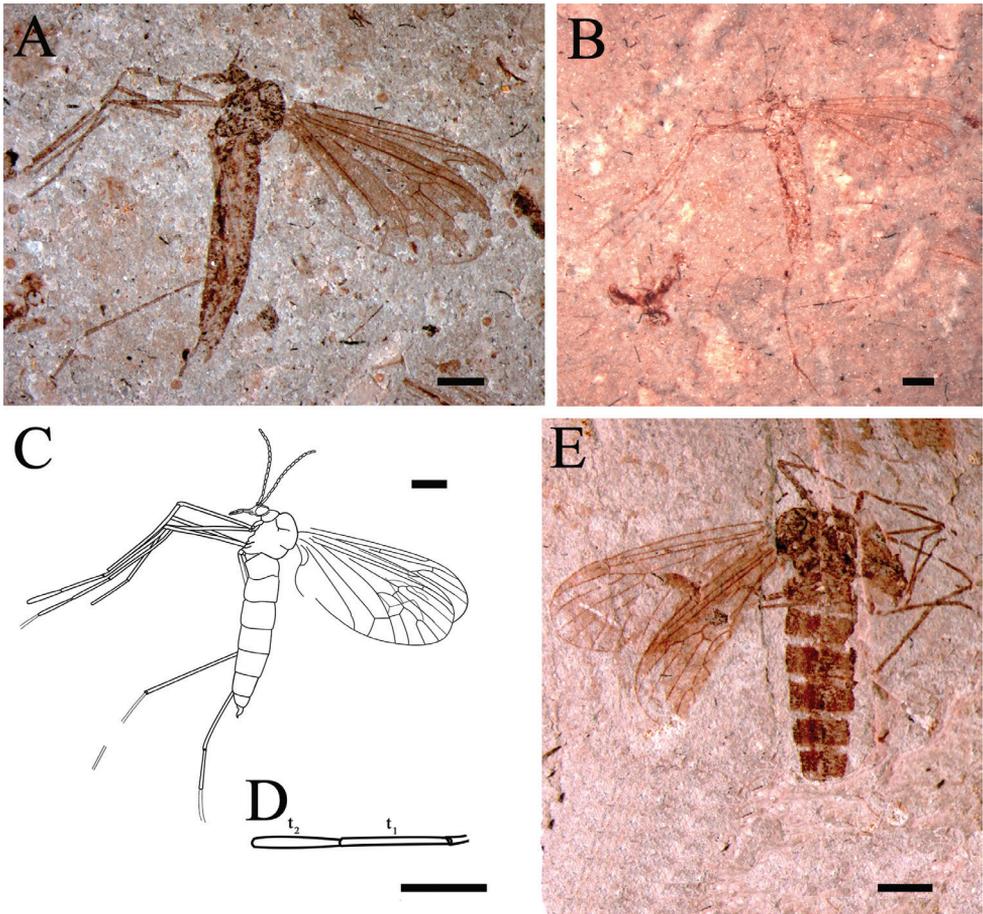


Figure 4. *Eotrichocera* (*Archaeotrichocera*) *amabilis* sp. n. Holotype, specimen CNU-DIP-NN2013134 **A** Photograph **B** Photograph, under alcohol **C** Line drawing **D** Tarsus of the mid leg. Paratype, specimen CNU-DIP-NN2013132 **E** Photograph. Scale bars = 1 mm; t_1 = the first segment of tarsus; t_2 = the second segment of tarsus.

nation clear, Sc rather short about 0.71 times as long as the wing and terminating clearly proximad of R_2 ; crossvein sc-r locating at 1/3 [Paratype 1/2] of Rs, and distad to the Sc ending; [Paratype Rs arising about one-fourth from the base of the wing]; Rs forking at 0.55 [Paratype 0.64] times of wing length; R_{2+3} about 1.9 times as long as R_{2+3+4} ; R_2 about 0.18 of length of R_3 ; R_3 almost 3.7 times as long as the R_{2+3} ; R_5 9.0 times as long as R_{2+3+4} ; M_1 1.6 times of the dM_{1+2} ; crossvein m-m well developed about 0.73 times as long as bM_3 , closing the d-cell and nearly 0.17 [Paratype 0.21] times as long as wing; bM_{1+2} nearly 2.1 times as long as the length of the r-m and the latter at one-fourth of the d-cell; d-cell broad ($W/L=0.58$ [Paratype 0.56]) and almost 0.17 times of length of wing; Cu long, curved (angle about 121°) and reaching the wing posterior margin at 0.67 from the base of the wing; the stem of A divided into A_1 and A_2 ; A_1 long, slightly curving and

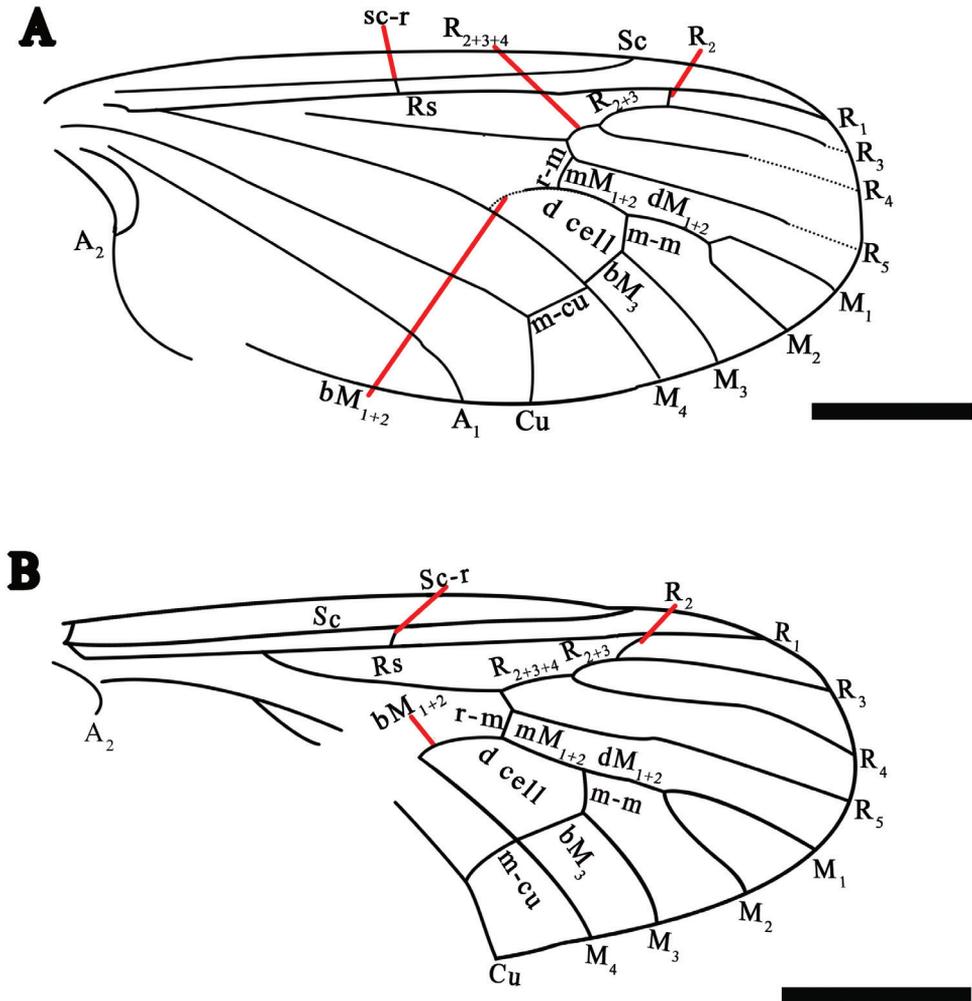


Figure 5. *Eotrichocera* (*Archaeotrichocera*) *amabilis* sp. n. Holotype, specimen CNU-DIP-NN2013134 **A** Line drawing of left wing. Paratype, specimen CNU-DIP-NN2013132 **B** Line drawing of left wing. Scale bars = 1 mm.

reaching the wing posterior margin; A_2 short, 0.13 times as long as wing and almost 0.25 times as long as length of A_1 , bending sharply and reaching the wing posterior margin.

Abdomen: Abdomen relatively long and thin, with ten segments. Female genitalia discernible (Figs 4A–C) [Paratype genitalia indiscernible].

Legs: Legs slender and long; the hind leg nearly 1.5 times as long as the abdomen and 1.4 times as long as the wing. Tarsus with five segments; the first segment of tarsus (t_1) is 1.2 times as long as t_2 in mid leg.

Remarks. The new species is compared and differentiated from all other species in *Eotrichocera* (*Archaeotrichocera*) in Table 2.

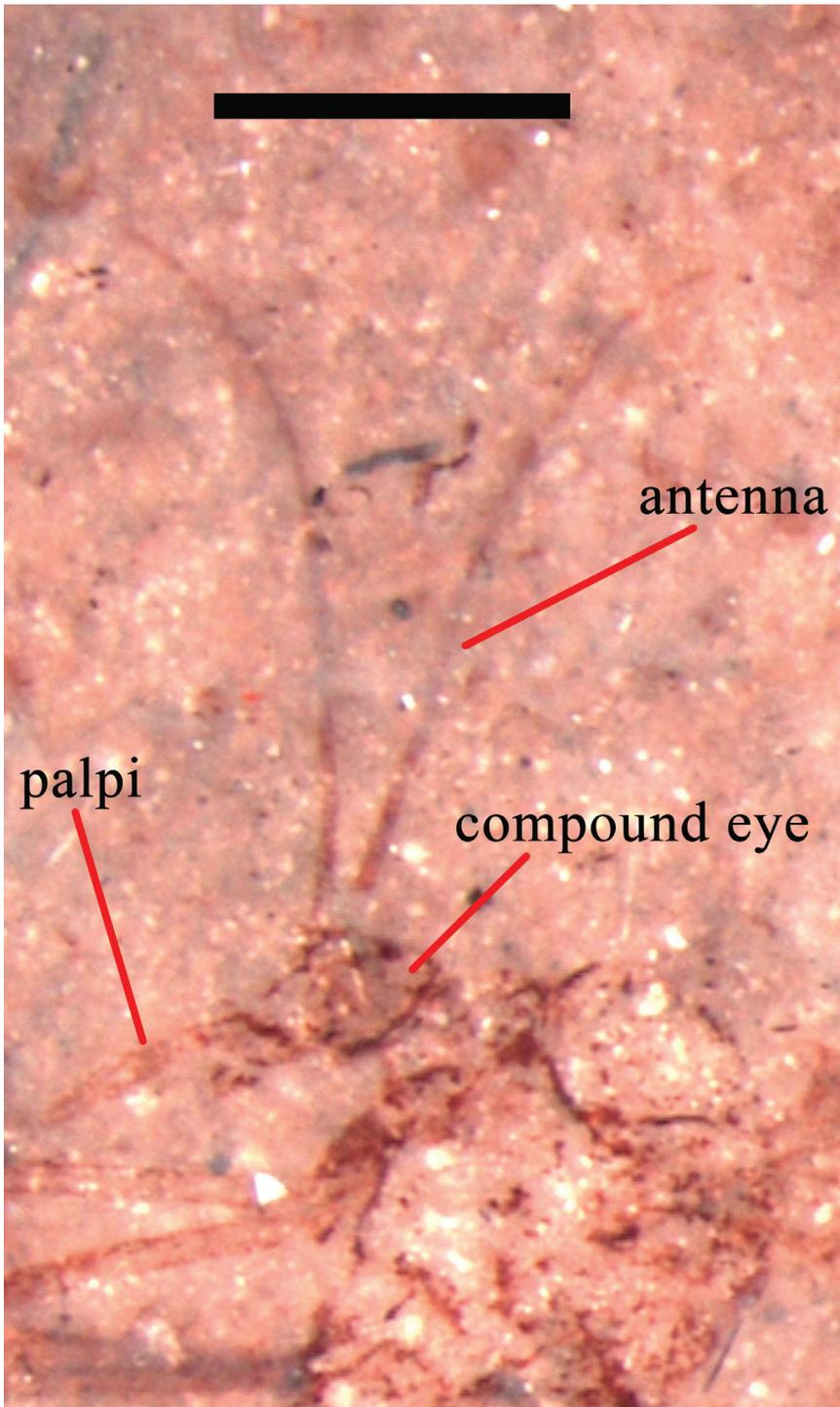


Figure 6. *Eotrichocera (Archaeotrichocera) amabilis* sp. n. Holotype, specimen CNU-DIP-NN2013134, Photograph of head, under alcohol. Scale bar = 1 mm.

Due to limitation of fossil preservation, some of the morphological characters of previously described fossil are not objective or clear. We set up an aforementioned key based on the Sc length and ending location at anterior margin, wing length, crossvein sc-r position, Rs forking location and A₂ length, to differentiate the species of subgenus *Archaeotrichocera*. These characters may help future morphological and taxonomic studies in differentiating fossil species of Trichoceridae.

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